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The algae of Lightfoot's *Flora scotica*

Peter S. Dixon

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The algae of Lightfoot's *Flora scotica*

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Synopsis

Lightfoot's *Flora scotica* (1777) is of importance as it was the first flora of the northern parts of the British Isles to use Linnaean binomials. Although Lightfoot left no statement of his method of work, deductions can be made from a comparison between his publication and his algal herbarium, facilitating typification of the 18 new binomials for which Lightfoot provided diagnoses. The correct name for the alga currently known as *Polyneura gmelinii* is *P. laciniata* (Lightf.) P. Dixon, comb. nov.

Introduction

The *Flora scotica* of the Reverend John Lightfoot (1735–1788) is of importance as it was the first flora of the northern parts of the British Isles in which Linnaean binomials were used. The flora treated all groups of plants, and is of considerable importance phycologically because of the 18 species of algae for which new binomials were published. Several of these provide basionyms of names in the current checklist (Parke & Dixon, 1976).

The flora represented the results of a tour of Scotland made in 1772 in the company of Thomas Pennant, who has given a detailed account (Pennant, 1776). Pennant encouraged Lightfoot to write *Flora scotica*, and the work was subsequently printed and published at Pennant's expense. The date of publication has been the source of some confusion, but Price (1968) has analysed the causes of this and concluded that the flora was published in 1777. It contains 35 plates, of which eight are of algae. Of the algal plates, most were prepared by Sowerby, although one (pl.XXVIII) is attributed to Robertson and another (pl.XXXIII) is anonymous.

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The history of the Lightfoot Herbarium after the death of its collector in 1788 is complicated; Britten (1915) and Dixon (1959) have described the sequence of ownership. As a result of the work of Britten, part of the Lightfoot Herbarium was discovered at the Saffron Walden Museum in 1913, and transferred to the Royal Botanic Gardens, Kew (K) in 1915. The need to locate early algal collections for the preparation of *Seaweeds of the British Isles* led to a general survey of herbaria in 1957–60, and it was discovered in the course of this that no algae, fungi, or lichens had been involved in the transfer of the Lightfoot Herbarium from Saffron Walden to K. Search had shown in 1957 that there were then about a dozen Lightfoot algal specimens in the general algal herbarium at K, and a further six specimens at the British Museum (Natural History) (BM). Detailed consideration of the history of the Lightfoot Herbarium suggested that the missing portions must still be housed at Saffron Walden Museum and, indeed, the algae were found there in an attic in 1958 (Dixon, 1959). Portions of the Lightfoot Herbarium (comprising the lichens, fungi, and the genus *Byssus*) are still missing, not having come to light in the searches of 1958. The Lightfoot algae were transferred on permanent loan from Saffron Walden Museum to K in 1958, and subsequently (with other algal material) to BM in 1970 (Brenan & Ross, 1970).

In 1791 Goodenough received permission from Queen Charlotte (wife of King George III), the then owner of the Lightfoot Herbarium, to examine it. Finding it in a damaged condition, he suggested that it be looked over by a competent authority and Smith was selected for this task. Smith made extensive use of the Lightfoot Herbarium in his various publications on phanerogams, but he appears to have paid little attention to the algal sheets as no annotations in his hand have been detected. Goodenough, however, examined some algal portions of the Lightfoot Herbarium in detail, and in his treatment of the genus *Fucus* (as then understood) made frequent reference to Lightfoot material (Goodenough & Woodward, 1797). Goodenough relabelled many of the folders and rearranged the material of *Fucus*, but did little or nothing with the genera *Conferva* and *Ulva*. It is obvious that Goodenough was permitted to keep specimens (see p. 10, under *Fucus repens*), and he incorporated them into his personal herbarium, which was transferred to K in 1880. Thus, the few Lightfoot algal specimens prior to 1958, together with an unknown number of Lightfoot specimens of groups other than algae received from Goodenough, possibly accounted for early opinions that the Lightfoot Herbarium was at K.

Following the discovery of the Lightfoot algae at Saffron Walden, each of the original flimsy Lightfoot species folders was placed in a strong manila folder for added safety but no rearrangement was undertaken. Thus, the algae of the Lightfoot Herbarium are in as near original state as possible, apart from the rearrangement of *Fucus* undertaken by Goodenough.

Since the transfer of the Lightfoot algae to K and thence to BM, several authors (Chapman, 1972; Dixon, 1960, 1962; Norton & Burrows, 1969; Prud'homme van Reine, 1972) have typified Lightfoot binomials on the basis of the material now at BM.

The algal descriptions given by early authors, such as Hudson and Lightfoot, are imprecise by modern standards, so that critical typification of the names of new taxa is imperative. This requires an understanding of the materials used, and also of the author's philosophy and method of work. In the case of Lightfoot, these were not stated explicitly although they can to some extent be deduced.

Herbaria are cited by their official abbreviations:

BM:	British Museum (Natural History), London;
BM-K:	Specimens formerly in the Herbarium of the Royal Botanic Gardens, Kew, and now at the British Museum (Natural History), London;
K:	The Herbarium, Royal Botanic Gardens, Kew;
OXF:	Fielding-Druce Herbarium, The University, Oxford.

Analysis of Lightfoot's method of work

Lightfoot left no statement of his method of work. As with his contemporary Hudson (Irvine & Dixon, 1982), it is possible to analyse the text and deduce the philosophy and practice used. In the case of Lightfoot the situation is simpler than for Hudson because much of the algal herbarium is intact and comparisons can be made with the published text. A complete catalogue has been prepared of the Lightfoot algal herbarium to facilitate such comparisons.

The textual arrangement adopted in *Flora scotica* was similar to the earlier publications of Linnaeus (1753, 1763, 1767, 1771) and Hudson (1762). For each species, a polynomial diagnosis in Latin was provided, with the specific epithet placed in the margin. In many cases, the Lightfoot polynomial was taken with little or no modification from Linnaeus or Hudson. The diagnosis was followed by a list of synonyms, both pre-Linnaean and binomial. Lightfoot differed from Hudson in that he quoted Linnaean and Hudsonian synonyms exclusively in binomial form, whereas Hudson used the polynomial form most frequently (Irvine & Dixon, 1982). Hudson considered quotation of a synonym with illustration of much value as a means of interpretation, and Lightfoot did this even more extensively, citing previously published illustrations of Morison (1699), Réaumur (1712), Oeder (1766–1771), Gmelin (1768), Gerard (1636), Gunnerus (1766, 1772), Buxbaum (1728), Micheli (1729), and Dillenius (1742). In connection with the last author, Lightfoot (1777: xv) acknowledged that he had consulted the actual herbarium, whereas there is no direct evidence that Hudson had done so (Irvine & Dixon, 1982). Presumably, Lightfoot also examined the Morison herbarium at Oxford (OXF) at the same time, although he does not mention this.

One significant difference between the work of Hudson and Lightfoot is that the latter gave extensive discussions of the occurrence, use, and systematic relations of all species in English, rather than Latin, a practice which he justified in the preface (Lightfoot, 1777: xi).

Lightfoot gave new binomials to three types of entries:

1. In cases such as *Conferva equisetifolia* (p. 17), *Fucus verticillatus* (p. 10), and *Ulva laciniata* (p. 12), Lightfoot did not cite any synonyms at all, and he regarded these as new species.
2. In cases such as *Conferva confragosa* (p. 5), *Fucus polyschides* (p. 9), and *Ulva crispa* (p. 11), Lightfoot cited one or more pre-Linnaean polynomials in synonymy, so that the Lightfoot binomial was based on a combination of his own material (if, in fact, he had any) and the material on which the pre-Linnaean polynomial was based. Such a binomial validates a species as 'new' by modern standards, but Lightfoot did not consider it so because he was not discriminating between pre-Linnaean polynomials and binomials.
3. In cases such as *Conferva corallina* (p. 5) and *Fucus nereideus* (p. 9), Lightfoot cited one or more binomials in synonymy, so that his names are superfluous and illegitimate (Art. 63 of Stafleu *et al.*, 1978).

Understanding these categories facilitates typification of the Lightfoot binomials.

Cataloguing the algal herbarium showed that Lightfoot had specimens from other parts of the British Isles numerically more extensive than those from Scotland. Some of these had been collected personally on one or other of the many tours which Lightfoot made to various parts of the British Isles (cf. Riddelsdell, 1905), while others had been received from correspondents. Very few of the specimens in the Lightfoot Herbarium are dated, and information as to the place of collection is usually scanty. At least half the specimens bear no indication of the place of collection at all, and in many other cases it consists only of an indication of the county from which the specimen was obtained. Dates of collection are also rare. Because of these difficulties it is often not possible to establish whether a specimen was collected on the Scottish tour or, if not, whether the specimen was in Lightfoot's possession prior to that tour or incorporated afterwards.

In the introduction to *Flora scotica*, Lightfoot acknowledges that he received considerable help in the course of his tour from various Scottish botanists, who contributed information, and, in a few cases, specimens. From the text of *Flora scotica*, and from annotations on algal specimens in the Lightfoot Herbarium, it would appear that Thomas Yalden 'a late student of physic at Edinburgh' was the most prolific contributor of Scottish specimens.

The Lightfoot Herbarium contains numerous specimens which are referred to unpublished binomials, particularly from Ellis or Solander. It is not clear whether the specimens in question were received from Ellis or Solander, or merely referred by Lightfoot to an unpublished species name emanating from Ellis or Solander. There is no evidence in the form of annotations to suggest that they were *identified* by either Ellis or Solander.

Sir Thomas Frankland, who had worked with Hudson (see Irvine & Dixon, 1982), was probably the most prolific of all Lightfoot's contributors. Despite the fact that they were contemporaries, there is no evidence of any direct collaboration between Lightfoot and Hudson. For example, there are no specimens annotated by Hudson in the Lightfoot Herbarium, although several are annotated by Frankland as having been 'named by Hudson, from his own mouth'. Moreover, the only references to *Flora scotica* (Lightfoot, 1777) are in the appendix to the second edition of Hudson's *Flora anglica* (Hudson, 1778), and not in the main text. Obviously, *Flora scotica* was published before Hudson was aware of its contents, by which time the second edition of *Flora anglica* had been set.

A significant discovery arising from this investigation is that certain species treated in *Flora scotica* apparently do not occur in Scotland. An example of this is *Fucus nereideus* (see p. 9). In other cases, such as *Fucus polyschides* (see p. 9), the Scottish origin of the material used in the original treatment is suspect, although absolute proof is lacking. Presumably, Lightfoot was travelling light on his tour of Scotland and collecting relatively little material. He based the inclusion of these entities on memory rather than on a specimen in hand. This would account for some curious discrepancies in geographical distribution noted during the preparation of forthcoming parts of *Seaweeds of the British Isles*.

Typifications of Lightfoot's new algae

The following notes refer to the typification of new binomials coined by Lightfoot, listed alphabetically, initially by genus and then by species.

1. *Byssus purpurea* Lightfoot (1777: 1000)

Lightfoot described *Byssus purpurea* on the basis of material collected 'Upon the base of the abbot *Mackinnon's* tomb, in the ruin'd abbey at *I. Columb-kill*' [= Iona, Argyll, Scotland]. He also cited a reference to an illustration by Micheli (1729), with a query '*Michel. Gen. p.* 211. *n.* 13. *tab.* 90. *f.* 2?'. As indicated previously, the fungi, lichens, and the genus *Byssus* of the Lightfoot Herbarium are still missing, not having been found during the searches at Saffron Walden in 1913 and 1958. Neither has any Lightfoot specimen referred by him to *Byssus purpurea* been located in any other herbarium. Therefore, as indicated in Dixon & Irvine (1977), typification of *B. purpurea* Lightf. on the basis of material is not possible at present. Furthermore, the citation of the reference to Micheli (1729) with a query means that *B. purpurea* Lightf. cannot be typified by his material.

Specimens were obtained by various collectors from the type locality within a few years of Lightfoot's visit. Although subsequent collection from a type locality may or may not represent an accurate re-collection of the original material, the present species does represent a special case as the type locality is unique. Reconstruction of the abbey at Iona during the present century involved re-roofing the chancel and cleaning the interior, which was in ruins at the time of Lightfoot's visit. The late Dr K. M. Drew visited the cathedral in 1948 in an effort to establish the identity of *Byssus purpurea* Lightf., but there was then no trace of algae on the tomb, which is in the re-roofed part. She was able to collect material corresponding to Lightfoot's alga from a wall between the refectory and the cloisters in the still unreconstructed part of the abbey (Drew, personal communication).

Byssus purpurea Lightf. is the basionym of *Audouinella purpurea* (Lightf.) Woelk. This species occurs in various habitats in the British Isles (Dixon & Irvine, 1977) and is extremely polymorphic. The alga described by Lightfoot represents the low-growing stunted form found on maritime rock above high water: the species develops to much greater size on intertidal rocky shores.

2. *Conferva confragosa* Lightfoot (1777: 976)

The Lightfoot treatment of *Conferva confragosa* is as follows: 'CONFERVA filamentis mucosis simplicibus æqualibus violaceis. – a *Linnæo* non descripta. (*Dillen. musc.* 15. *t.* 2. *f.* 4.)', with the further comment 'We observ'd it upon the rocks in the waterfalls on the mountain of *Goatfield*; in the isle of *Arran*, &c.' The Lightfoot treatment is based therefore on material personally collected (if not actually preserved) and on the entity described previously by Dillenius (1742).

The Lightfoot Herbarium does not have a folder annotated as *Conferva confragosa*. No Lightfoot specimen so annotated has been found elsewhere in the Herbarium or in any other herbarium.

The Dillenian Herbarium at OXF contains a specimen annotated '*Conferva mucosa confragosis rivulis innascens*' which represents the Dillenian material of the entity referred to by Lightfoot. This material can therefore be regarded as lectotype of *Conferva confragosa*: it was selected as such by Drouet (1968) and referred by him to *Microcoleus irriguus* (Kütz.) Drouet, a blue-green alga.

3. *Conferva corallina* Lightfoot (1777: 988)

The Lightfoot treatment of *Conferva corallina* is as follows: 'CONFERVA filis geniculatis dichotomis. *Syst. nat. edit.* 13. *p.* 818. CONFERVA *corallinoides*. *Sp. pl.* 1636. (*Dillen. musc.* 33. *t.* 6. *f.* 36. *et ejus varietas minor, t.* 6. *f.* 37. CONFERVA *geniculata. Ellis. Philos. Transact. vol.* 57. *t.* 18. *fig. f. F. opt.*'

Conferva corallina Lightf. is thus a superfluous and illegitimate name, antedated by the two previously-described species cited in the original treatment (*Conferva corallinoides* Linnaeus, 1753 and *Conferva geniculata* Ellis, 1767), and it must be typified from the type materials of the earliest name. All binomials refer to the alga known currently as *Griffithsia corallinoides* (L.) Batters.

4. *Conferva diaphana* Lightfoot (1777: 996)

Lightfoot described *Conferva diaphana* as a new species, in his sense of that term, with neither pre-Linnaean nor binomial synonyms cited. He stated that it occurred 'Upon rocky shores, in basons of water left by the tides, and often adhering to Fucuses'.

The Lightfoot Herbarium contains a single folder annotated 'Conferva diaphana' in Lightfoot's hand which contains six specimens (or packets containing specimens); no Lightfoot specimens have been discovered elsewhere. From the annotations on these six specimens it would appear that one was collected at Bognor (Sussex), two at Scarborough (Yorkshire) by Frankland, while two are completely unannotated. The sixth specimen is annotated 'Conferva Diaphana. Fl: Caledon: & Ellis & Solander' in Lightfoot's hand, but it is not clear whether this annotation implies that this specimen served as the basis for the description of *Conferva diaphana* in *Flora scotica*, or whether it is a specimen collected subsequently outside Scotland and merely identified by Lightfoot as belonging to the species which he had previously described. This specimen has been accepted provisionally as the lectotype of *C. diaphana* Lightf., and a series of illustrations of it is presented (Figs 1 & 2).

Conferva diaphana is the basionym of *Ceramium diaphanum* (Lightf.) Roth, and its attribution has been the subject of great controversy (cf. Du Rietz, 1930; Kylin, 1909; Petersen, 1908, 1911; Sjöstedt, 1928; Svedelius, 1927, 1929). The often polemic literature has resulted from the considerable unrecognized morphological plasticity in the genus *Ceramium,* and a failure to follow correct typification procedures. The illustrations of the material accepted as the provisional lectotype of *Conferva diaphana* Lightf. should help to resolve problems with respect to the application of that name. Although it is unfortunate that the evidence is not indisputable that the specimen selected was used as the basis for the original diagnosis, that specimen was at least referred by the original author to the entity under discussion.

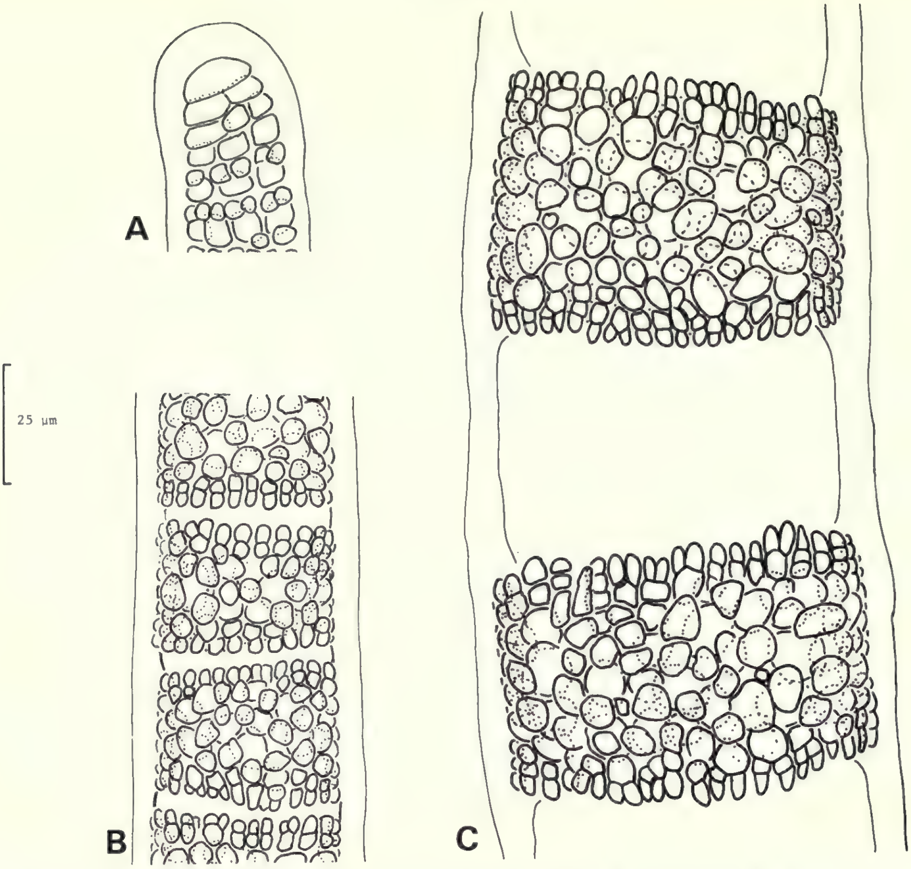

Fig. 1 Provisional lectotype material of *Conferva diaphana* Lightf. A. Apex. B. Portion of axis, 20 segments behind the apical cell. C. Portion of axis, 80 segments behind the apical cell.

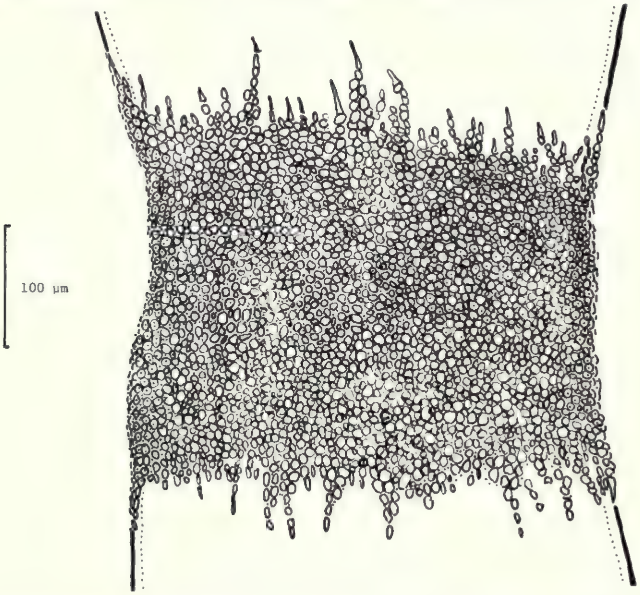

Fig. 2 Provisional lectotype of *Conferva diaphana* Lightf. A cortical band in a mature portion of an axis.

5. *Conferva equisetifolia* Lightfoot (1777: 984)

Lightfoot described *Conferva equisetifolia* as a new species, in his sense of that term, with neither pre-Linnaean nor binomial synonyms cited. He stated that it occurred 'In the Frith of *Forth*, but rare. A specimen was communicated by Mr. *Yalden*. The same we also found on the coast of *Cornwall*, and at the rocks call'd the *Needles*, near the isle of *Wight*.'

No trace of the Yalden specimen has been found, either in the Lightfoot Herbarium or elsewhere. The Lightfoot Herbarium contains a single folder annotated 'Conferva equisetifolia', with several loose specimens and a label on which there is an illustration and a diagnosis written in Lightfoot's hand. The diagnosis on the label is slightly different from that published, but its presence, together with the rough illustration, suggest that this was the material used by Lightfoot in his treatment. The annotation on the label concludes 'ad littora Insula Vectis prope rupes Needles dictae. a Dom.Woods Clerico.' It would seem appropriate to consider this material as being of type status and a lectotype has been selected from it. The material is referable to the alga known currently as *Halurus equisetifolius* (Lightf.) Kütz.

Although the attribution of *Conferva equisetifolia* Lightf. has never been questioned by subsequent authors, it is extremely doubtful if a specimen of *Halurus equisetifolius* could have been collected in the Firth of Forth. Hooker (1821) and Greville (1824) both accepted the occurrence of the species in that area on the basis of Lightfoot's statement, although strong doubts were expressed by Harvey (1846). Present knowledge indicates that *Halurus equisetifolius* occurs as far north as Argyll on the west coast of Scotland, but that it is absent from east Scotland, having its northern limit in the North Sea in Yorkshire.

6. *Conferva nodulosa* Lightfoot (1777: 994)

The Lightfoot treatment of *Conferva nodulosa* is as follows: 'CONFERVA filamentis geniculatis ramosissimis, articulis nodulosis, fructificationibus tuberculatis lateralibus. – CONFERVA *elongata* ? *Huds. Fl. Angl.* 484. *n.* 25. (*Dillen. musc.* 35. *t.* 6. *f.* 38'. He further states that it occurs 'On the sea shores frequent, often adhering to Fucuses', but cites no specific locality.

It is therefore evident that *Conferva nodulosa* Lightf. is based on material observed or collected personally, together with the Dillenian illustration and/or material. The punctuation of Lightfoot's treatment is such that the query could be interpreted as applying only to *Conferva elongata* Huds., or to both that and the Dillenian reference, as the original description of *C. elongata* (Hudson, 1762) cites the same Dillenian reference. As Lightfoot had examined the Dillenian Herbarium while Hudson apparently had not, the most appropriate interpretation of Lightfoot's treatment, and of his expression of doubt, is that he was using his knowledge of the Dillenian Herbarium to interpret *C. elongata* Huds. As discussed elsewhere (Irvine & Dixon, 1982) there are grounds for thinking that Hudson included several discordant elements in his initial concept of *C. elongata*. The Lightfoot Herbarium contains several specimens of *C. elongata* which confirm the current application of that epithet to a species of *Polysiphonia*, and one of these is annotated 'Hudson named this for Mr Frankland at different Times'.

The Lightfoot Herbarium contains nine folders annotated as '*Conferva nodulosa*' in Lightfoot's hand, and a single unannotated folder containing further material identified by Lightfoot. These folders contain numerous specimens which all appear to have been collected in England (Sussex, Hampshire, Dorset, and Cornwall); there is no sign of any specimen indisputably collected in Scotland. No specimens referred by Lightfoot to *C. nodulosa* have been detected in other herbaria. All specimens are referable to the genus *Ceramium* and most to the alga known currently as *C. rubrum* (Huds.) Agardh, a specimen of which has been accepted provisionally as the lectotype of *Conferva nodulosa* Lightf.; it should be appreciated that this specimen was collected in Sussex, not Scotland.

From this it might seem that *Conferva nodulosa* Lightf. might simply be dismissed as a synonym of *C. rubra* Huds., the basionym of *Ceramium rubrum* (Huds.) Agardh. *Conferva rubra* Hudson (1762: 486), however, is a superfluous and illegitimate name because of a reference in the synonymy in the protologue to *Fucus cartilagineus* Linnaeus (1753: 1161), the basionym of *Plocamium cartilagineum* (L.) P. Dixon. Thus, an alternative name must be found for the alga known currently as *Ceramium rubrum*, one of the best-known binomials used in the red algae. Consequently, accurate typification of taxonomic synonyms published shortly after *Conferva rubra* Huds. is of great importance.

7. ***Conferva verticillata*** Lightfoot (1777: 984)

Lightfoot described *Conferva verticillata* as '*species non descripta*', i.e. as a new species, with neither pre-Linnaean nor binomial synonyms cited. He stated that it occurred 'Amongst the sea rocks, in basons of water left by the tides, in the Frith of *Forth*, and many other places, not unfrequent'.

The Lightfoot Herbarium contains several specimens, of which two small packets are particularly relevant; no material has been detected in any other herbarium. The two packets are annotated as follows:

(a) 'my Conf: verticillata Fl: Scot: Examine & compare it with C: spongiosa', in Lightfoot's hand.

(b) 'my Conf: spongiosa Fl: Scot: I described it as it appear'd thro' a small Magnifier, but I now think it verticillata', in Lightfoot's hand.

Both specimens are of the alga known for many years as *Cladostephus verticillatus* (Lightf.) Agardh, although recently Prud'homme van Reine (1972) reduced it in status to *C. spongiosus* f. *verticillatus* (Lightf.) P. van Reine. The first specimen (a) listed above is selected here as the lectotype of *Conferva verticillata* Lightf. The lectotypification by Prud'homme van Reine (1972) does not precisely indicate which of the Lightfoot specimens is being selected.

8. ***Fucus endiviifolius*** ['*endiviæfolius*'] Lightfoot (1777: 948)

Lightfoot described *Fucus endiviifolius* as a new species, in his sense of that term, with neither pre-Linnaean nor binomial synonyms cited. He stated that it had been collected 'In the Frith of *Forth*, and on the coast of *Iona*' and provided an illustration (Lightfoot, 1777: pl.XXXII f, g) prepared by Sowerby.

The Lightfoot Herbarium contains two folders labelled by Lightfoot as *Fucus endiviifolius*, one of which contains two specimens collected by Frankland at Scarborough with no indication of relevance to the original treatment. The second folder contains a single mounted specimen (for which the published illustration is a perfect mirror image) together with a diagnosis and instructions to the artist. These are as follows: 'The Fructifications are visible near the Margins. Draw this of the natural Size, & put it in a Plate with another small one'. This specimen is clearly the holotype of *F. endiviifolius* and it is referable to the alga known currently as *Cryptopleura ramosa* (Huds.) Kylin ex Newton. Because of the excellent illustration there have been no uncertainties as to the attribution of *Fucus endiviifolius* Lightfoot during the past two centuries.

Although it is not possible to be certain whether the specimen was collected at one or other of the localities cited, or from elsewhere, this is of little importance, since *Cryptopleura ramosa* is of widespread occurrence throughout the British Isles.

9. ***Fucus ligulatus*** Lightfoot (1777: 946)

Lightfoot described *Fucus ligulatus* as a new species, in his sense of that term, as he was unable to refer it to either a pre-Linnaean polynomial or a binomial name. He stated that it occurred 'In the Frith of *Forth*, about *New-Haven*, and other places, but not common', and provided an illustration (Lightfoot, 1777: pl.XXIX) prepared by Sowerby.

The Lightfoot Herbarium does not now contain any folder annotated as *Fucus ligulatus*; no relevant material occurs in other folders nor has any Lightfoot material been discovered elsewhere. In the absence of material, *F. ligulatus* Lightf. must be typified by the illustration mentioned above (cf. Chapman, 1972), which is of the alga known currently as *Desmarestia ligulata* (Lightf.) Lamouroux.

Nomenclatural studies of the genus *Desmarestia* (e.g. Pease, 1917, 1920; Setchell & Gardner, 1924, 1925; Chapman, 1972) have failed to appreciate that *Fucus ligulatus* Lightf. is an illegitimate name because it is a later homonym of *F. ligulatus* S. Gmelin (1768), which is referable to the alga known today as *Calliblepharis jubata* (Gooden. & Woodw.) Kütz. The next epithet for the alga known currently as *Desmarestia ligulata* is *herbacea*, derived from *Fucus herbaceus* Hudson (1778: 582). Although initially described by Hudson independently of *F. ligulatus* Lightf., the synonymy of these two entities was accepted by Hudson (1778, Appendix: 662) thus rendering *F. herbaceus* superfluous (Art. 63.1). Subsequently, Turner (1809) described independently another species of *Desmarestia* under the name *Fucus herbaceus* which is thus an illegitimate name because it is a later homonym of the illegitimate *Fucus herbaceus* Hudson. Lamouroux (1813) transferred *F. herbaceus* Turn. to *Desmarestia* in his original treatment of that genus so *Desmarestia herbacea* Lamouroux (1813: 45) must be regarded as a new name (Art. 72, Note 1). In the same way *Desmarestia ligulata* Lamouroux (1813: 45) must also be regarded as a new name. It is the oldest name available for the alga under discussion, and lectotypified by the illustration of *Fucus ligulatus* provided by Lightfoot (1777: pl.XXIX).

10. ***Fucus nereideus*** Lightfoot (1777: 956)

Lightfoot described *Fucus nereideus* on the basis of material collected 'In the Frith of *Forth* and other places, but not common', but also made reference to two previously-published binomials, *F. sericeus* S. Gmelin (1768) and *F. spinosus* S. Gmelin (1768). *Fucus nereideus* Lightf. is therefore a superfluous and illegitimate name, which must be typified from the Gmelin material of these two species. Although both have been considered frequently to be referable to the genus *Gelidium* (cf. J. Agardh, 1851), this is unlikely in the case of *F. sericeus* as there are no species of *Gelidium* reported from its place of collection (Kamtschatka). Other workers (cf. Harvey, 1849) have regarded *F. sericeus* as a species of *Ptilota*, and this is a more likely attribution. However, Gmelin material is not available for further study at the present time.

The material in the Lightfoot Herbarium identified as *Fucus nerideus* is of *Pterocladia capillacea* (S. Gmelin) Bornet & Thuret, a species restricted in the British Isles to southern and western shores. This indicates once again that the material of the Lightfoot Herbarium could *not* have originated in the Firth of Forth (Dixon, 1960).

11. ***Fucus polyschides*** Lightfoot (1777: 936)

Lightfoot described *Fucus polyschides* on the basis of material collected 'Upon the sea-shores . . ., but not common, as at *I-Columb-kill* [= Iona, Argyll, Scotland], &c' and comments further that 'We have observ'd the same also in *South Britain*, upon the coast of *Cornwall*, where it grows so large that a single specimen is sometimes a load for a man's shoulders'. He also refers to the illustration by Réaumur (1712) of *F. arboreus polyschides* (from which, no doubt, the epithet was derived) and the illustration of *Fucus palmatus* given by Gmelin (1768) '*sed non omnia synonyma*'. Gmelin referred the alga figured and described to *F. palmatus* L. (= *Palmaria palmata* (L.) Kuntze), but it is clearly conspecific with that described subsequently by Lightfoot.

The Lightfoot Herbarium contains two folders, both of which are annotated in Goodenough's hand 'Fucus bulbosus Huds. – [Fucus] polyschides Lightfoot', each containing a single loose specimen. Associated with one specimen is a label annotated in Lightfoot's hand 'Cornwal Stalks F: polyschides.', while the labels with the other are annotated, also in Lightfoot's hand: 'Cornwal a new Species' 'My F. polyschides or furbellowed Fucus'.

Fucus polyschides is the basionym of *Saccorhiza polyschides* (Lightf.) Batters. Norton & Burrows (1969) accepted the argument (Dixon, 1960) that not all algae described in *Flora scotica* were based on Scottish material, and typified *Fucus polyschides* by the second specimen mentioned above, collected in Cornwall, England.

12. ***Fucus prolifer*** Lightfoot (1777: 949)

Lightfoot described the entity as 'F. frondibus submembranaceis dichotomis catenato-proliferis, apicibus dilatatis bifidis' with the questioned attribution to it of two previously-published entities 'FUCUS *crispus* ? *Syst. nat. edit.* 13. *p.* 815. *et Huds. Fl. Ang. p.* 472 ?', together with a reference to an illustration by Buxbaum (1728: pl. 60, fig. 2). The species was said to occur 'Upon the shores of the western coast, adhering to shells and stones' and Lightfoot provided an illustration (pl.XXX), prepared by Sowerby, showing a whole plant at natural size and two fragments magnified.

No material referred by Lightfoot to *Fucus prolifer* occurs anywhere in the Lightfoot Herbarium and none has been discovered elsewhere. Lightfoot achieved some notoriety for copying illustrations apparently without acknowledgement (cf. Price, 1968), although the magnified illustrations (which are original) suggest that he must have had access to material of *F. prolifer* which is now lost. It was suggested (Dixon, 1962) that *Fucus prolifer* Lightf. should be lectotypified by the Lightfoot illustration, and no additional information has come to light subsequently to change this view.

Because of the excellent illustration provided by Lightfoot, there has been little uncertainty over the attribution of *Fucus prolifer* Lightf. to the alga known variously as *Phyllophora epiphylla* (Müll.) Batters, *P. rubens* Grev., or correctly *P. crispa* (Huds.) P. Dixon (Dixon, 1962). Lightfoot's *F. prolifer* is a later homonym of *F. prolifer* Forskål (1775), which is a species of *Caulerpa*.

13. ***Fucus repens*** Lightfoot (1777: 961)

Lightfoot described *Fucus repens* on the basis of material which 'grows upon the sea-rocks, which are wash'd by the waves, in many places, particularly near *Musselburgh*, &c', and he also refers to a Dillenian illustration (Dillenius, 1742) '*Dillen. musc.* 50. *t.* 10. *f.* 9. A. B. C. D. *bon.*'.

The Lightfoot Herbarium includes three folders containing several specimens, and a further specimen originating from Lightfoot has been detected at BM-K. One specimen in the Lightfoot Herbarium is enclosed in a packet annotated 'Fucus repens of Yalden near Musselborough. It seems to be that Tremella described by Dillen: t. 10 f. 9 sed Queere' in Lightfoot's hand and 'Fucus repens I gathered this near Muselborough what do you call it it creeps along on the Stones which it covers' in an unknown hand, possibly that of Yalden. The Dillenian entity to which reference is made is his '*Tremella marina caespitosa, segmentis tenuibus*' (Dillenius, 1742: 50). All the specimens identified in the Lightfoot Herbarium as *Fucus repens* and the Dillenian alga are referable to the species of *Catenella* which has been known by various names during the present century: *C. opuntia* (Gooden. & Woodw.) Grev., *C. repens* (Lightf.) Batters, and correctly, *C. caespitosa* (With.) L. Irvine. The specimen described above, possibly collected by Yalden, has been selected as the lectotype of *Fucus repens* Lightf.

A Lightfoot specimen of *Fucus repens*, once at K and now at BM, was received at the former as part of the Goodenough collections. It is associated with a label annotated 'Her Majesty is very glad that this little Specimen may be of Some use to Dr. Goodenough, and desires him to Keep it. Her Majesty will also give commission to Mr. Agnus to Search for the fucus that is wanting, in case it had got among other things'. As mentioned previously, Goodenough worked on the Lightfoot Herbarium while it was in the possession of Queen Charlotte. It is curious, therefore, that Goodenough & Woodward (1797) should have described as *Fucus opuntia* the same entity described previously by Lightfoot as *F. repens*, because, in this case, Goodenough had not only examined the Lightfoot Herbarium but actually had a portion of the Lightfoot material in his possession.

14. ***Fucus verticillatus*** Lightfoot (1777: 962)

Lightfoot described *Fucus verticillatus* as a new species, in his sense of that term, with neither pre-Linnaean nor binomial synonyms cited. He stated that 'We found it sparingly upon the rocks of the *Little Isles* of *Jura*', and provided an illustration (Lightfoot, 1777: pl.XXXI) prepared by Sowerby.

The Lightfoot Herbarium contains several specimens, one of which resembles the illustration

(Lightfoot, 1777: pl.XXXI) except that the artist omitted some of the major axes. This specimen is with two other specimens in a folder with a loose label. The specimen is annotated 'Fucus verticillatus. Fl. Scot.', while the label reads 'Fucus (verticillatus) frondibus tubulosis subarticulatis ramosis ramis verticillatis subulatis setaceo-ligulatis. In this the Branches are verticillate as in Horse-tail or Equisetum. The Fructifications are red Spots in the Substance of the Leaves near their Summits, but these I fear cannot be shown. Let him draw it just as it appears, of the Size of Nature', both in Lightfoot's hand. The other specimens in the Lightfoot Herbarium are annotated as having been collected in Yorkshire or Cornwall, but there is no real evidence to indicate that the illustrated specimen was collected in Scotland. As the illustration in *Flora scotica* is clearly based upon it, although admittedly as a somewhat simplified representation, it would seem best to select this specimen as the lectotype of *F. verticillatus*. The specimen is of the alga known currently as *Chylocladia verticillata* (Lightf.) Bliding.

One curious aspect is the Goodenough & Woodward (1797) were unable to locate the type material stating (p. 208) 'We have received specimens of this plant . . . under the name of F. *verticillatus of Mr. Lightfoot.* It is a matter of great regret to us that we could not meet with his original specimen.' A later comment (p. 233) states that 'Mr. Lightfoot's F. *verticillatus* unfortunately had been mislaid, so that no opportunity offered of proving that species from his original specimen'.

That *F. verticillatus* Lightf. was the oldest name for the common European species of *Chylocladia* was not appreciated for many years, the alga being known generally as *C. kaliformis* (Gooden. & Woodw.) Hook. The priority was first accepted by Bliding (1928), and again independently by Papenfuss (1947).

15. ***Ulva cornuta*** Lightfoot (1777: 972)

The Lightfoot treatment of *Ulva cornuta* is as follows 'ULVA subrigida cornuta terrestris. – (*Dillen. musc.* 52. *t.* 10. *f.* 13.)'. He further comments 'It is about an inch long, sometimes two or three; divided deeply, without order, into various acute horned segments; the edges turn'd inwards, otherwise a flat membrane. It is of a pale-green color, and substance somewhat rigid'. The diagnosis given by Lightfoot differs somewhat from that given by Dillenius (1742) which is '*Tremella terrestris cornuta*'.

The Lightfoot Herbarium does not now contain any folder annotated as *Ulva cornuta* and no relevant specimen has been found in any other herbarium. A specimen in the folder annotated '*Ulva montana*' in Lightfoot's hand may be relevant, however. This consists of a minute fragment of material in a packet annotated 'No 1 this I had from Scotland for the Tremella verrucosa. I am doubtful Please to dilute it and try what you can make of it', in an unknown hand, and 'Ulva cornuta. Fl: Scot: but possibly may be a Sponge or Zoophyte', in Lightfoot's hand. The Lightfoot annotation suggests that this is a specimen received after the publication of *Flora Scotica*, and not part of the material on which the original treatment was based. Identification of this material proved to be impossible.

The material in the Dillenian Herbarium at OXF referred to by Lightfoot is also unidentifiable. It consists of a scrap of material which Batters (in Druce & Vines, 1907) interpreted as 'possibly a fungus'; personal investigation suggested that Batters' interpretation was probably correct. Thus, one element cited by lightfoot in the protologue of *Ulva cornuta* is unidentifiable, as is also the specimen now in the Lightfoot Herbarium which may or may not be the material referred to by Lightfoot.

Neither of the specimens bears any close resemblance to the comments made by Lightfoot, cited above, which if anything suggest that *Ulva cornuta* Lightf. could have been a lichen. It is possible that after the publication of *Flora scotica* the original material of *U. cornuta* was moved by Lightfoot within his herbarium from the algae to the lichens, which are still missing.

16. ***Ulva crispa*** Lightfoot (1777: 972)

Lightfoot described *Ulva crispa* as follows: 'ULVA tenera crispa terrestris. – *Raii synop. p.* 64.

n. 12. (*Dillen, musc.* 52. *t.* 10. *f.* 12. A. B. C. D.)', with the further comment 'This is found lying upon the ground in shady places, at the foot of walls and houses'. Lightfoot's treatment was based therefore on his own material and on the entities described previously in Ray (1724) (which was in fact prepared by Dillenius) and by Dillenius (1742). The Lightfoot diagnosis differs slightly from the diagnoses of both Ray ('*Ulva terrestris tenerrima, viridis crispa*' and Dillenius ('*Tremella terrestris tenera, crispa*').

The Lightfoot Herbarium does not now contain any folder annotated as *Ulva crispa*. A specimen which appears to be the original Lightfoot material of *U. crispa* occurs in the Herbarium in the folder annotated *Ulva montana*. This specimen is enclosed in a packet annotated 'No. 22. In moist shady places on the North side of Walls where no Grass grows, generally', in an unknown hand and 'Ulva terrestris tenerrima viridis crispa. R. Syn: 64. not mentioned by Linn: or Huds: This of Ray may be no other perhaps than varietas ß of Ulva Lactuca. Hud:', in Lightfoot's hand. On the reverse of the packet is the annotation 'This is a thin membranaceous substance, & I think it mostly is where people Pisses agst. Walls.', in an unknown hand. This material is of the alga known currently as *Prasiola crispa* (Lightf.) Kütz. No other material of *Ulva crispa* originating from Lightfoot is known to exist elsewhere at the present time.

Examination of the Dillenian Herbarium at OXF reveals that there is a relevant specimen filed in the herbarium of the *Historia muscorum*. This was identified by Batters (in Druce & Vines, 1907) as *Prasiola crispa* and personal examination confirms this determination.

From the original Lightfoot treatment, and from the material in the Lightfoot Herbarium, it would appear that *Ulva crispa* was based principally on Lightfoot's own material, even though it is known that Lightfoot had consulted the Dillenian Herbarium. The slight changes in diagnosis between Lightfoot's treatment and those of Ray and Dillenius also support this view. Consequently, the specimen in the Lightfoot Herbarium has been selected as the lectotype of *Ulva crispa*.

17. ***Ulva laciniata*** Lightfoot (1777: 974)

Lightfoot described *Ulva laciniata* as a new species, in his sense of that term, with neither pre-Linnaean nor binomial synonyms cited. He stated that 'We gathered it upon the coast of *Iona*'.

The Lightfoot Herbarium contains one folder annotated 'Ulva laciniata' in Lightfoot's hand which contains a single specimen and a separate label. The label is annotated 'Ulva laciniata. I-columb-kill.', in Lightfoot's hand. The specimen bears a lengthy annotation in Lightfoot's hand, with instructions to his artist, as follows: 'Ulva (laciniata) frondibus planis purpureis, apice dilatitatis laciniatis undulatis. With a Microscope you may see the Seeds lodged in the Substance of the Membrane near the Edges, appearing like fine Grains of a red Powder. These I fear cannot be express'd. Draw the Plant of the Size of Nature just as it appears.' This specimen bears a close resemblance to the illustration published by Lightfoot (1777: pl.XXXIII), prepared by an unknown artist. No relevant material has been detected in any other herbarium.

The specimen on which the published illustration was based is considered the holotype of *Ulva laciniata* Lightf.

The identity of *Ulva laciniata* Lightf. has been the subject of much confusion. It appears that Hudson (1778) was the principal cause in that in the appendix to the second edition of *Flora anglica* he made the comment (Hudson, 1778: 652) 'Obs. *an varietas* Ulvae umbilicalis'. Subsequently, C. Agardh (1824: 190) listed *Porphyra laciniata* (Lightf.) Agardh as the first species of his newly created genus *Porphyra*. Later authors followed this attribution without question until Drew (1955: 3) suggested that *Ulva laciniata* might be a member of the Delesseriaceae, and rejected its application in *Porphyra*. Following the discovery and initial examination of the alga in the Lightfoot Herbarium the opinion expressed by Drew was confirmed (Dixon, 1959).

Detailed examination of the type material of *Ulva laciniata* Lightf. showed that it belongs to the alga known as '*Nitophyllum gmelinii* Grev.' or '*Polyneura gmelinii* (Lamouroux) Kylin', the basionym of which is *Delesseria gmelinii* Lamouroux (1813: 124). Since Lamouroux cites *Fucus palmetta* Gmelin (1768) as a synonym, *Delesseria gmelinii* is illegitimate, having the same type as the former (see Silva, 1952, and Guiry, 1977). However, the species described by Gmelin has been assigned elsewhere, so that the alga which has been called *Nitophyllum* or *Polyneura gmelinii* is without a name. *Ulva laciniata* Lightf. provides an epithet for the taxon, and its correct name therefore becomes ***Polyneura laciniata*** (Lightfoot) P. Dixon, **comb. nov.** (= *Ulva laciniata* Lightfoot 1777: 974).

18. ***Ulva montana*** Lightfoot (1777: 973)

Lightfoot described *Ulva montana* as 'ULVA plana coriacea terrestris sanguinea' as a new species in his sense of that term, with neither pre-Linnaean nor binomial synonyms quoted. He stated that it occurred in various localities: 'It grows upon the ground amongst the grass and moss on the sides of the mountains in the isle of *Skye*, and in *Ross-shire* on the side of a mountain call'd *Cail-veg*, between *Loch-broom* and *Lead-beg*, on the western coast, and doubtless in many other such-like places'.

The Lightfoot Herbarium contains a folder annotated *Ulva montana* in Lightfoot's hand which contains clumps of material, a label, and two packets which are not relevant to *U. montana* (see *Ulva crispa* and *Ulva cornuta*). The label is annotated 'Mountain Dulse Skye. Ulva montana. Fl. Cal.' in Lightfoot's hand: the specimen has been shown to Dr Francis Drouet and has been identified by him as *Anacystis montana* (Lightf.) Drouet & Daily.

The publication in which *Ulva montana* Lightf. was transferred to *Anacystis* (Drouet & Daily, 1952) made no mention of type material, although the subsequent, more detailed, treatment (Drouet & Daily, 1956) indicated that the type (of unspecified status) occurred at K, *prior* to the discovery of the Lightfoot Herbarium at Saffron Walden and its transfer to K. Search of the BM-K collections has failed to find the material referred to by Drouet & Daily (1956). Under these circumstances, it would seem best to regard the specimen in the Lightfoot Herbarium as the lectotype of *Ulva montana* Lightf.

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A taxonomic study of the lichen genus *Micarea* in Europe

Brian John Coppins

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A taxonomic study of the lichen genus *Micarea* in Europe

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Synopsis

A taxonomic revision is presented for the lichen genus *Micarea* in Europe, with special emphasis on those species occurring in the British Isles. In brief, this genus is here circumscribed to include most crustose lichens with lecideine (biatorine) apothecia, a poorly defined excipulum (sometimes absent altogether) of radiating paraphysis-like hyphae, a non-granular epithecium, *Lecanora*-type, 8-spored asci, simple to multiseptate, hyaline ascospores, and a 'grass-green' phycobiont usually of the so-called 'micareoid' type. Comparisons and possible relationships with similar genera are discussed. Noteworthy discoveries made during this study include the finding of cephalodia in three species, dimorphic paraphyses in several species, and a wide array of anamorphic forms, with three species each found to have three conidial states. Type studies have been made for nearly all names known, as well as those suspected, to be referable to *Micarea* in its present, wider concept. Forty-five species are recognised, of which 31 are confirmed from Britain. Seven species are new to science: *Micarea adnata, M. curvata, M. hedlundii, M. muhrii, M. nigella, M. olivacea,* and *M. myriocarpa* Vězda & V. Wirth ex Coppins. Several described species are included in *Micarea* for the first time, and additional name changes are required for nomenclatural reasons; nine new combinations result: *M. assimilata* (Nyl.), *M. crassipes* (Th.Fr.), *M. elachista* (Körber) Coppins & R. Sant., *M. globulosella* (Nyl), *M. intrusa* (Th.Fr.) Coppins & Kilias, *M. lignaria* var. *endoleuca* (Leighton), *M. melaenida* (Nyl.), *M. melanobola* (Nyl.), and *M. subviolascens* (Magnusson). Several taxa are excluded from the genus and the new combinations, *Psilolechia clavulifera* (Nyl.) and *Bacidia prasinata* (Tuck.), are proposed. Keys for the identification of all the accepted European taxa are given. The taxonomic parts are preceded by an outline of the historical background to the study of *Micarea*, and details of materials and methods employed in this study. Detailed accounts of the morphology, chemistry, and ecology in the genus are provided, and a discussion of distributions is supported by maps for the British taxa. All *Micarea* species occur on acidic, nutrient poor substrata, and most are confined to cool-temperate, boreal, or oceanic regions; a few occur in arctic-alpine areas but the genus is poorly represented in dry, lowland, Mediterranean regions. Prior to this study, most of the species were little-known or misunderstood; clarification of their taxonomy has been achieved by paying particular attention to their anamorphic states, chemistry (including pigmentation), and detailed anatomy. Consideration of the distribution and ecology of the species has proved invaluable in ordering the taxonomic chaos which previously surrounded the notoriously variable species of the genus.

Historical background

Lecideaceae

Until recently the circumscription of the *Lecideaceae* (and of the genera within it) had changed little from that adopted by Zahlbruckner (1926). It included most lichens with the following combination of characters: a crustose to squamulose thallus, a 'grass-green' phycobiont (excluding *Trentepohlia* and *Phycopeltis*), ± immersed to sessile, disc-like apothecia without a thalline margin, mainly colourless spores, and an absence of parietin (or related pigments) and (or) polarilocular spores. The principal genera in the family (e.g. *Lecidea, Catillaria, Bacidia, Biatorella, Mycoblastus, Lopadium, Bombyliospora*, and *Toninia*) were separated mainly on the basis of spore characters, i.e. size, septation, and number per ascus. This classification largely ignored many features which (according to modern mycological concepts) now merit careful consideration, although they were used to varying degrees for the delimitation of species or infrageneric categories above this rank. In brief, these features involve the structure of asci, excipular and hypothecial tissues, paraphyses and anamorphs, ontogeny, finer aspects of thallus structure, and nature and location of pigments and lichen substances. In addition, investigations of the phycobiont(s) and considerations of ecology and phytogeography often provide valuable supplementary information. However, the use of some of these features in an attempt to define more natural genera is not a purely recent phenomenon. Several lichenologists working in the 1850s and 1860s made bold attempts in this direction. With regard to the *Lecideaceae s. lat.*, two lichenologists deserving special mention are G. W. Körber (who introduced *Lecidella, Lopadium, Pyrrhospora, Schaereria, Schadonia,* and *Steinia*) and A. B. Massalongo (who introduced *Catillaria, Psilolechia, Sarcosagium, Scoliciosporum, Strangospora,* and *Toninia*). In the latter half of the 19th century lichenology came under the almost monarchical influence of William Nylander, whose simplistic generic concepts gained precedence over the more far-sighted works of Körber, Massalongo, and others. From the 1870s right up to the 1950s there were few attempts to reassess the generic concepts of Nylander or the slightly more complex, but no less artificial, system of Zahlbruckner. Between about 1929 and 1954 the French lichenologist M. G. B. Choisy resurrected many of the old and more or less forgotten genera, and created several new ones (e.g. *Haplocarpon [= Huilia], Hypocenomyce, Trapelia*, and *Tremolecia*). Unfortunately, Choisy's works made little impact at the time and it was not until the mid-1960s that lichenologists began to look more carefully at the delimitation of genera. Recent investigations have led to the reinstatement (although often with emendations) of many of these genera and many new genera have had to be described (e.g. *Fuscidea, Herteliana, Melanolecia, Trapeliopsis, Tylothallia*, and *Vezdaea*). Most are included in the key to European lichen genera in Poelt & Vězda (1981). Despite the many advances made during the last 15 years, it will be several decades before a reasonably natural generic classification within the *Lecideaceae s. lat.* is achieved. The enormity of the task can be appreciated from the fact that Zahlbruckner (1921–40) accepted no less than 1450 species in the genus *Lecidea* alone! In addition to the high number of taxa involved, further problems arise from the locating and obtaining on loan suitable (including type) material, and the many difficulties in observing and interpreting many microscopical, morphological, and ontogenetic features.

Micarea

The genus *Micarea* was first validly described in 1825 by Elias Fries in his *Systema orbis vegetabilis* (see p. 96), and was placed in his 'Tribus Collemaceae' on account of its rather gelatinous thallus, although he noted that it had *Lecidea*-like apothecia. The generic name was little used by most 19th century lichenologists, although it was accepted with the single species (*M. prasina*) by a few such as Körber (1855). Towards the end of that century, J. T. Hedlund submitted his doctoral thesis to the University of Uppsala. In this work (Hedlund, 1892) he adopted and emended the genus to include 20 species, and his circumscription of the genus is essentially the same as that accepted by Vězda & Wirth (1976) and myself, although many species have since been added. Hedlund's sagacious work was evidently too revolutionary for his time, and it did not achieve international recognition. It seems that Hedlund was disillusioned and had difficulties in finding a position. He turned to horticulture (especially dendrology) and then became an authority on *Sorbus*. Although Hedlund's obvious talents were not lost to botany, they were sadly lost to lichenology, especially the study of microlichens.

Vězda & Wirth (1976) slightly expanded Hedlund's concept of *Micarea* by including *Lecidea sylvicola* and related species (all without 'micareoid' algae), and also *Bacidia beckhausii*. Apart from the exclusion of *B. beckhausii,* my own concepts are much the same, although I have emended the genus very slightly so as to include species such as *Lecidea (Helocarpon) crassipes* and *Catillaria intrusa*.

The first species of *Micarea* to be described was *Lecidea [Micarea] lignaria* Ach. (1808). By 1850 only seven of the currently accepted 45 European species were validly published. At about this time lichenologists began to make use of better quality microscopes and the additional characters they revealed. By the end of the nineteenth century 34 of the accepted species had been described. The European *Micarea* flora was increased by only one species (*Lecidea subviolascens*) between 1900 and 1960. In 1961 Vězda published *Bacidia [Micarea] subleprosula*, and as a result of the present studies (some in collaboration with Mr P. W. James, Dr A. Vězda, and Dr V. Wirth) a further nine species have been described. In the future a few additional species will probably be added to the European flora, but the greatest expansion within the genus will come from the study of extra-European collections; indeed, many European, undescribed, and described (in other genera) species are already known to me from parts of the world outside Europe.

Materials

During the course of this study I have examined about 3,000 specimens (*c.* 1800 from the British Isles) attributable to *Micarea*, plus a further *c.* 500 specimens which have been referred to other genera. Material has been received on loan from (or studied in) the following institutional herbaria: ABD, ANGUC, BEL, BERN, BG, BM, BON, C, DBN, DEE, DUKE, E, G, GLAM, GZU, H, HAMU, HBG, HFX, IMI, K (now in BM; cited as BM ex K), L, LD, LIV, LSR, M, MANCH, NMW, NWH, O, S, STD, STU, SUN, TUR, U, UPS, VER, WCR, WIS, WRSL; abbreviations according to Holmgren *et al.* (1981). In addition, numerous specimens have been received on loan from private herbaria. From the British Isles these are: Dr H. J. M. Bowen (Oxford), Dr R. W. M. Corner (Penrith), Mr I. P. Day (Carlisle), Dr U. K. Duncan (Arbroath; lichen herbarium recently gifted to E), Dr A. Fletcher (Leicester), Mr V. J. Giavarini (Parkstone, Dorset), Dr O. L. Gilbert (Sheffield), Mr R. Gomm (Taunton), Rev. G. G. Graham (Hunwick, Co. Durham), Mr A. Henderson (Leeds), Dr C. J. B. Hitch (Saxmundham, Suffolk), Dr P. D. Hulme (Aberdeen), Dr A. R. Pentecost (Royal Tunbridge Wells), Dr F. Rose (Liss, Hampshire; many specimens now in BM), Dr M. R. D. Seaward (Bradford), Mr J. F. Skinner (Southend-on-Sea), Dr P. B. Topham (Dundee), Mr R. G. Woods (Newbridge on Wye, Powys); and from elsewhere in Europe: Dr J. Hafellner, Dr H. Mayrhofer, and Prof. Dr J. Poelt (all Graz, Austria), Mr L.-E. Muhr (Karlskoga, Sweden), Dr A. Vězda (Brno, Czechoslovakia), and Dr V. Wirth (Ludwigsburg, W. Germany).

When studying a group of much misunderstood lichens it is a rewarding exercise to investigate folders of other superficially similar (but strictly unrelated) taxa, especially those that occur in similar habitats. During this study numerous specimens of *Micarea* have been found in folders of widely misinterpreted ('dustbin') names, such as *'Bacidia sphaeroides'*, *'Catillaria erysiboides'*, and *'Lecidea vernalis'*.

Copies of the list of specimens examined have been lodged at BM, DBN, E, GZU, M, NMW, UPS and US.

Methods

Field studies

I have attempted to observe as many as possible of the accepted species in their natural habitats because such experience is invaluable for the appreciation of environmentally controlled variation and ecological requirements. For this end I have made field studies in most parts of mainland Britain, and also S.E. Ireland, Denmark (N. Jylland), mid- and N. Sweden. In addition, I have collected *Micarea* specimens during earlier expeditions to France (Bretagne) and western Ireland. I have been successful in finding two-thirds of the European species, and all but two (*M. assimilata* and *M. subleprosula*) of the 31 British species.

Light microscopy

Observations and measurements of external features were mostly made at ×50 using a Vickers stereomicroscope equipped with a measuring eyepiece. Internal features were investigated with a Wild M20 microscope which was fitted with a drawing tube and a 2·5× adapter for the drawing of spores and conidia etc. Most sections were made by hand with a razor blade, but some were cut by a freezing microtome. Sections were usually mounted in water, followed by (or directly in) 10% or 50% KOH(K), domestic bleach(C), 50% HNO_3, or ammoniacal erythrosin (0·5g erythrosin in 100 ml 10% ammonia solution), but other mountants such as cotton-blue in lactophenol (LCB), congo red, and alcian blue were also used at times. Tests for amyloid reactions were made by mounting directly in Lugol's iodine solution (1g iodine and 2g potassium iodide in 300 ml distilled water), or in this solution following treatment with 10% KOH. More permanent preparations were made by ringing mounts in LCB with nail varnish, or by mounting in polyvinyl alcohol (PVA) or cotton blue in PVA (see Omar *et al.*, 1979). For further details on techniques see also 'Guide to keys and identifications' (p. 100).

Thin-layer chromatography

The t.l.c. techniques employed were those described by Walker & James (1980) which are based on the standard method of Culberson (1972). For the purposes of routine analysis only two of the three basic solvent systems were found to be necessary (i.e. H.E.F. and T.D.A.).

Nomenclature

In the list of synonyms for a given species each entry begins with the oldest valid name (basionym) and is followed with later combinations included in Hedlund (1892), Smith (1911, 1926), and James (1965*a*), and some others which have important nomenclatural implications. Zahlbruckner (1921–40) and Lamb (1963) should be consulted for additional combinations. The entries are listed chronologically, except for entirely invalid (or illegitimate) and misapplied names which are included at the end of the lists.

Abbreviations of authors are according to Hawksworth (1980); those of journals to the third [1980] edition of *Serial Publications in the British Museum (Natural History) Library*; and those of books to Hawksworth (1974) or Stafleu & Cowan (1976–81).

Apart from those newly described in recent years, few names in *Micarea* have been formally typified (according to Art. 7 of the Code); all cited lectotypes and neotypes are selected in this work, unless otherwise indicated.

The nomenclature of lichens not treated in detail mainly follows Hawksworth *et al.* (1980), but a few later changes are used.

Morphology

Thallus

Thallus structure in *Micarea* is crustose and basically simple, but nevertheless, encompasses much interspecific and intraspecific variation. For the purposes of explanation thallus morphology can be roughly divided into five types. [Note: the discussion of the first type includes some general features applicable to all types.]

(i) *Areolate-type* (Fig. 1A–C)

The term areolae (pl.) is used here to describe discrete, rounded (when viewed from above), flattened, or more usually convex (sometimes ± globose) portions of the thallus which have developed directly from the prothallus lying in or on the substratum. These should be distinguished from the (often angular) segments derived from the cracking of a previously continuous crust. The areolae in *Micarea* mostly range from the 0·06 to 0.2 mm diam, but are characteristically larger in certain species. Thalli comprising smaller, discrete, granular, soredia-like structures (goniocysts) are dealt with in the next category (ii).

Species that have well-developed, convex areolae sometimes appear ± squamulose, e.g. *M. assimilata, M. incrassata, M. lignaria* (as in type of *Lecidea trisepta* var. *polytropoides*), *M. melaenida*, and *M. subviolascens. Catillaria zsakii* (a synonym of *M. melaenida*) was placed in the squamulose genus *Toninia* Massal. by Lettau, but its thallus is not truly squamulose and it was excluded from *Toninia* by Baumgartner (1979). In *M. subviolascens* (and to a lesser extent in some other species) the areolae become confluent and the resultant crust becomes secondarily cracked into 'islands' (each containing several primary areolae), thus giving the thallus a rather squamulose appearance. The areolae in most species are whitish or pale to medium grey, and often tinged dull greenish, bluish or brownish. The areolae of *M. lignaria* var. *endoleuca* are characterically ivory or cream-yellow. More vivid yellow, citrine or orange thallus colourations are not known in *Micarea*.

A few whitish, arachnoid, prothalline hyphae are sometimes visible in specimens with scattered areolae, but a thick prothallus as found, for example, in some species of *Phyllopsora* (Swinscow & Krog, 1981) is unknown in *Micarea*. The thallus in most *Micarea* spp. is effuse and wide-spreading, and even when thalli form small patches amongst other lichens, a delimiting hypothallus, such as found in many species of *Fuscidea* and *Lecidella*, is never formed. Small thalli forming ± circular patches amongst other lichens, suggesting parasitic behaviour, are characteristic of *M. intrusa* (p. 140).

In vertical section the areolae usually lack a well-defined cortex, but their surface is sometimes covered by a thin (*c.* 2–10 μm thick), hyaline amorphous layer which does not dissolve in concentrated KOH (Fig. 1A, C). Such a layer is found in the areolae of, e.g. *M. alabastrites, M. assimilata, M. cinerea, M. elachista, M. incrassata, M. lignaria, M. peliocarpa, M. subnigrata, M. subviolascens,* and *M. ternaria*. Areolae with a similar external appearance, but without an amorphous covering layer, can be seen in well-developed specimens of, for example, *M. denigrata, M. nitschkeana, M. globulosella*, and sometimes *M. melaena* (Fig. 1B). The thallus of these species (and to a lesser extent that of *M. elachista*) is often invaded and disrupted by the dematiaceous hyphae of a fungal parasite(s), and non-lichenized algae, resulting in a dark, often blackish, scurfy crust. This phenomen on is best exemplified by *M. melaena*, which in Britain is rarely found with a healthy, well-developed thallus. By contrast, during my excursions in Sweden I found it to be rarely parasitised. Susceptibility to invasion by parasites or opportunists may be related to climatic factors, being increased in the British Isles by the overall weather and warmer conditions. It would appear, therefore, that the amorphous covering layer (never present in *M. melaena*) is an effective barrier against potential invaders, but whether or not this is the reason for its evolution is a matter for speculation.

The nearest approaches to the development of a true cortex are found in *M. elachista* and *M. melaenida*. Sections of healthy areolae show an outer layer (*c.* 10–12 μm and 12–20 μm thick respectively) of compacted, evacuated hyaline hyphae (Fig. 1C). The amorphous covering layer of *M. elachista* often partially disintegrates causing the areolae to exhibit a white-pruinose appearance, a feature not noted in any other species of the genus.

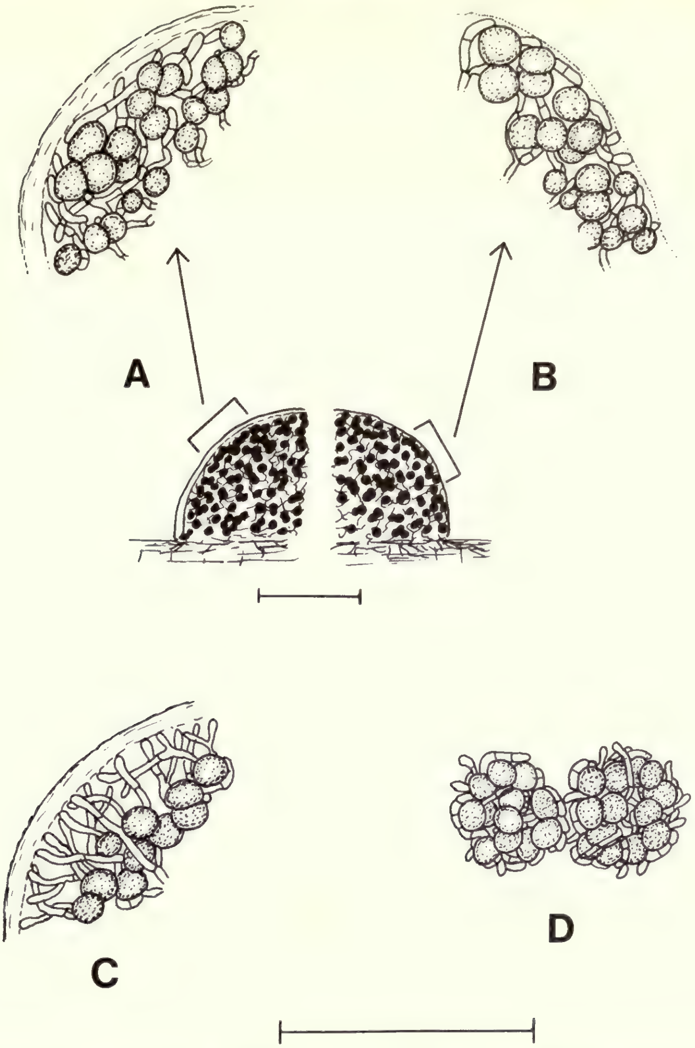


Fig. 1 Some thallus types in *Micarea*. **A**, areolate-type without cortex but with amorphous covering layer (e.g. *M. lignaria*). **B**, areolate-type without cortex or amorphous covering layer (e.g. *M. denigrata*). **C**, areolate-type with both cortex and amorphous covering layer (*M. elachista*). **D**, goniocysts (*M. prasina*). Scale = 50 μm.

The outermost hyphae of areolae are frequently coloured or surrounded by a pigment, usually that which is found in the upper hymenium of the apothecia, or the pycnidial walls, of the given species; for example, the dilute olivaceous, K+ violet pigment in *M. denigrata, M. elachista, M. globulosella, M. nitschkeana*, and *M. subviolascens*, the green, K−, HNO_3+ red pigment in *M. cinerea, M. lignaria, M. peliocarpa, M. sylvicola*, and *M. ternaria*, and the brown, K−, HNO_3− pigment in *M. subnigrata*. The intensity of pigmentation is much dependent on exposure to light and pigment may be entirely absent in shade forms. Species that always lack pigment in their apothecia and pycnidia (e.g. *M. alabastrites, M. pycnidiophora,* amd *M. stipitata*) similarly lack pigment in the thallus.

In the areolae of most species the algal layer is in direct contact with the substratum. However, a white medulla, devoid of algal cells, may be formed in the larger areolae of some species, e.g. *M. incrassata, M. intrusa, M. lignaria*, and *M. subnigrata*.

(ii) *Goniocyst-type* (Fig. 1D)

Several species have a finely granular thallus composed of discrete, ± globular structures, mostly *c.* 12–40 μm diam. These ecorticate granules consist of clustered algal cells intertwined and surrounded by short-celled hyphae, and are never protected by an amorphous covering layer. They are often seen to have short protruding hyphae, but they never have distinct spines as found in some species of *Vezdaea* (Poelt & Döbbeler, 1975). They are similar to soredia, but because they are the main component of the thallus and not derived from specialised structures (soralia) or eroding or disintegrating parts of a different thallus type (see (iii) below), the term goniocyst (Ozenda, 1963) seems the most applicable for them.

In *M. prasina, M. hedlundii,* and *M. melanobola* the thallus is composed entirely of goniocysts, the first of which appear to arise directly from the prothalline hyphae; further development is presumably by a process of division or budding from existing goniocysts. *M. botryoides* has a 'primary' thallus of flattened granular-areolae and in a few specimens I have noticed goniocysts developing from these areolae, which then become obscured as the goniocysts proliferate. However, in most specimens of *M. botryoides* no areolae can be seen; either they have become obscured or, perhaps in some cases the thallus develops as goniocysts from the outset.

In *M. prasina* and *M. melanobola* the outermost hyphae of superficial (exposed) goniocysts are often surrounded by the K+ violet pigment which also occurs in the upper hymenium of these species. When well developed, thalli composed of goniocysts have a ± gelatinous appearance when moist; this was the reason why Elias Fries originally placed the genus *Micarea* in his 'Tribus Collemaceae'.

The thallus of *M. synotheoides* consists of small dark granular-areolae and is somewhat intermediate between the 'areolate-type'. The thallus of *M. myriocarpa* sometimes has a scurfy appearance but is often organized into small (10–15 μm diam) goniocyst-like granules.

(iii) *Sorediate-type*

This is represented by the apparently closely related *M. leprosula* and *M. subleprosula*. Their thalli are essentially of the 'areolate-type' but their areolae lack an amorphous covering layer and are very fragile (easily broken by touching with the point of a needle), often breaking down or eroding to form irregularly shaped, pale green or yellowish green sorediał granules, *c.* 20–50 μm diam.

(iv) *Smooth- or scurfy-type*

Included here are thalli which, although developed on the surface of the substratum, are not organized into discrete areolae or goniocysts. The thalli may be smooth, continuous to rimose, or irregularly scurfy-granular. Such thalli may be formed by species that normally have well defined areolae (e.g. *M. lignaria* and *M. melaenida*) or, by lignicolous species whose thalli are often endoxylic (e.g. *M. anterior, M. nigella*, and *M. olivacea*). The thalli of *M. bauschiana* and *M. lutulata* vary from smooth or rimose, to scurfy-granular, and lack areolae, whereas the similar *M. lithinella*, *M. sylvicola*, and *M. tuberculata* sometimes produce areolae. Another two species whose thalli fall within this category are *M. adnata* and *M. turfosa.*

(v) *Immersed-type*

The thallus of many lignicolous species is indistinct and developed below the surface of the substratum, which may have a bleached appearance (cf. *M. muhrii*). An endoxylic thallus is occasionally formed by species that more characteristically have superficial areolae, e.g. *M. cinerea, M. denigrata, M. lignaria, M. muhrii,* and *M. peliocarpa*. Conversely, *M. melaeniza* and *M. misella* are usually endoxylic but forms with areolae are sometimes encountered. The thallus in *M. anterior, M. nigella*, and *M. olivacea* is often endoxylic, but a thin ± smooth crust is sometimes formed on the surface of the lignum.

The thalli of *M. contexta, M. eximia*, and *M. rhabdogena* are invariably endoxylic. Sections of the substratum show small goniocyst-like clusters (*c.* 15–40 μm diam) surrounded and interconnected by pigmented hyphae. As in the relevant examples in thallus types (i–iii), and in *M. turfosa* in group (iv), the pigment involved is that found in the upper hymenium or pycnidial walls of the given species, viz.: dark green and K− in *M. contexta* and *M. eximia*, and olivaceous and K+ violet in *M. rhabdogena*.

The species which at times grow on bryophytes usually have a superficial thallus, but even so, the thallus is often, in part, endocuticular. When on bark *Micarea* thalli are generally epiphloeodal, but at least partially endophloeodal thalli have been seen in *M. cinerea* and *M. peliocarpa*.

Phycobionts

Among the 45 species of *Micarea* accepted in this revision three types (? genera) of 'grass-green' phycobiont can be distinguished by LM observations on thallus squashes. Unfortunately the identities of these algae are unknown and they await critical studies by an algologist. In addition, two genera of blue-green alga may be involved in the formation of cephalodia (*q.v.*).

The commonest alga in *Micarea* is that found in the type species (*M. prasina*) and was discussed at some length by Hedlund (1892, 1895). In the course of this study this alga is hereafter referred to as 'micareoid' (Fig. 2). Its cells are fairly regular in appearance, ± globose, thin-walled and *c.* 4–7 μm diam. Reproduction within the thallus appears to be by a process of cell division in which the protoplast divides in two, followed by the laying down of a dividing wall which joins up with existing wall of the parent cell (Fig. 2A). No internal divisions into aplanospores as found in, for example, *Myrmecia* and *Trebouxia*, have been observed. Contact between the fungal hyphae and the algae cells is by intracellular haustoria (Peveling, 1974) which are readily seen at ×1000 (mounted in 10% KOH, followed by ammoniacal erythrosin). The haustoria may be peg-like (Fig. 2B, D–E), swollen to become clavate (Fig. 2G) or capitate (Fig. 2C, H), or spreading into a foot (Fig. 2F). In collapsed algal cells (Fig. 2H) the haustoria are intensively stained. A characteristic feature of the micareoid alga and its relationship with the mycobiont is that a hypha frequently becomes closely aligned along the dividing line of two separating algal daughter cells (Fig. 2D–E); the hypha concerned is often seen to penetrate one or both of the cells by haustoria.

The second algal type is found in *Micarea sylvicola* and its presumed relatives *M. bauschiana*, *M. lutulata*, and *M. tuberculata*. The cells are thin-walled and irregular in size and shape, varying from 5–12 μm diam when globose to up to *c.* 15×10 μm when ± ellipsoid. I am undecided as to their mode of reproduction within the thallus. The large number of cells at the lower end of the size range is suggestive of aplanospore formation, but I have never observed a mother-cell undergoing division. Haustorial penetrations by the mycobiont hyphae have been detected, but they are never as distinct as those involving micareoid algae or the phycobiont of *M. intrusa* (see below).

The third algal type is confined to *M. intrusa*, and has large globose cells, 7–21 μm diam, with thick hyaline walls *c.* 1–2μm thick. Cell division within the thallus seems to be by a process of the division of a mother-cell into three or four daughter-cells (i.e. 'protococcoid' division). Many of the cells are clearly seen to be deeply penetrated by a haustorium (Fig. 55). This phycobiont looks very similar to that of *Scoliciosporum umbrinum* and may well be identical with it.

Cephalodia

For reviews of the morphological, taxonomic, and physiological aspects of cephalodia see Jahns (1974), James & Henssen (1976), and Millbank (1976).

Cephalodia have been found in three species of *Micarea*: *M. assimilata, M. incrassata* and *M. subviolascens*. The first two species have thalli composed of verrucose areolae with a micareoid phycobiont. However, sections of their thalli reveal the presence of ± globose structures (*c.* 200–600 μm diam) containing a blue-green alga of the genus *Nostoc*. In many cases these structures are visible externally and closely resemble the areolae except that they are brown, and usually darker, in colour. Internally they consist of numerous ramifying fungal hyphae (presumably belonging to the *Micarea*) and dense masses of *Nostoc* cells which have lost their normal (when free-living) filamentous arrangements; and I am in no doubt that these structures are cephalodia. I am less certain of the status of the more loosely organized clusters of *Stigonema* which are sometimes associated with the same two *Micarea* species, and also *M. subviolascens*. However, the *Stigonema* filaments are, at least partially, disrupted and fungal hyphae are present.

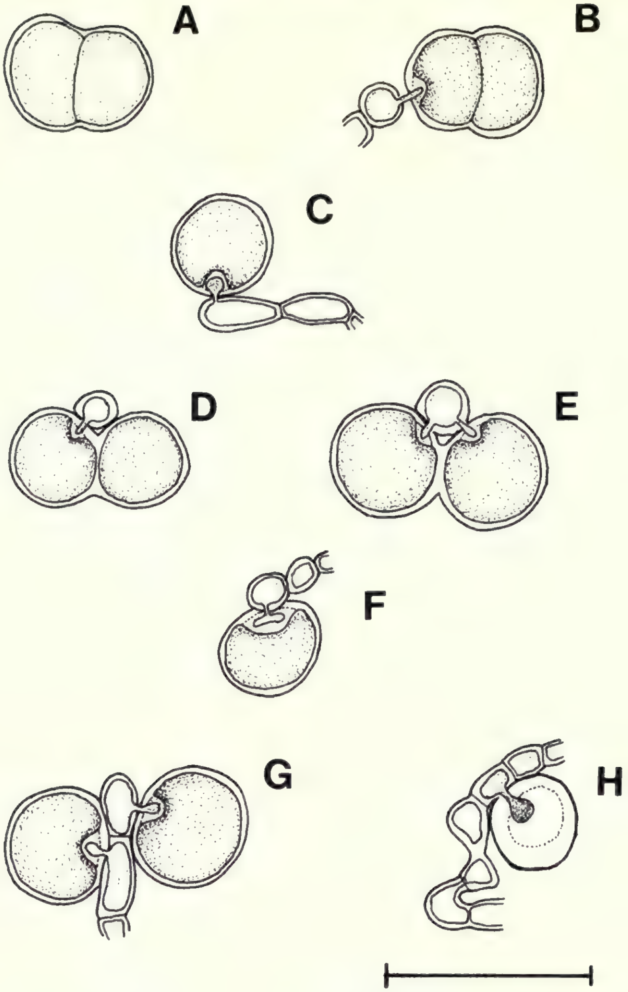


Fig. 2 'Micareoid' phycobiont of *Micarea alabastrites* and its relationship with mycobiont hyphae; see text for further details. Scale = 10 μm.

The three above-mentioned *Micarea* species are morphologically closely related and occur in exposed arctic-alpine situations. In such habitats the formation of cephalodia with a blue-green alga(e) which has the ability to fix atmospheric nitrogen, is of undoubted nutritional benefit to the mycobionts. Most morphological and physiological studies concerning cephalodia have involved macrolichens. Reports of cephalodia in crustose lichen are relatively few, although some are listed by James & Henssen (1976). Additional examples in the Lecideaceae include *Huilia aeolotera, H. elegantior, H. panaeola* (Hertel, 1977), and *Lecidea pallida* (Fries, 1874).

Apothecia: external features

As a rule the apothecia in *Micarea* are small to medium sized, convex to ± globose or tuberculate, and usually immarginate. However, this generalization encompasses considerable variation even within a single given species. With regard to shape, some species (e.g. *M. denigrata* and *M. prasina*) are very variable with apothecia that may be shallow-convex to convex-hemispherical (Figs 3A–B, 4A–B) and finally ± globose (Fig. 3D) or tuberculate (Fig. 3C). Apothecia of other species may be less variable: those of *M. alabastrites* and *M. cinerea* are broadly convex to hemispherical, sometimes tuberculate, but never ± globose; at the

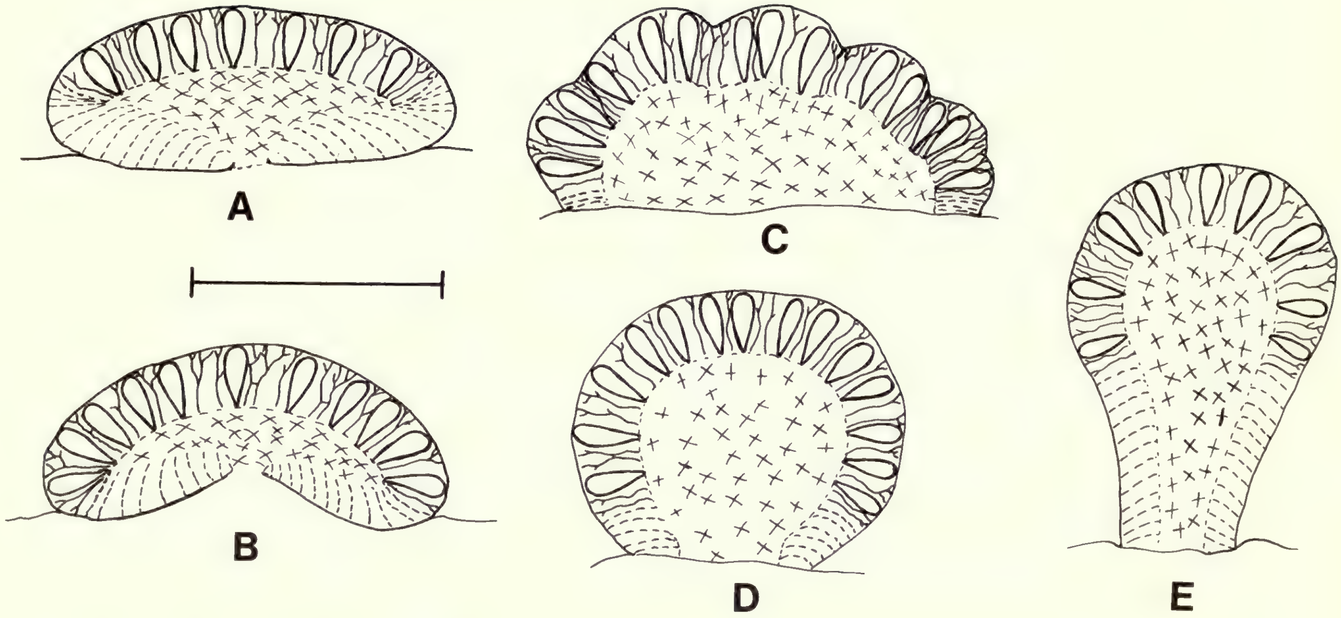


Fig. 3 Some apothecium types in *Micarea* (semi-diagrammatic). **A**, convex with well-developed excipulum (*M. peliocarpa*). **B**, ditto, but apothecium expanded and excipulum reflexed. **C**, ditto, but apothecium tuberculate. **D**, globose with reflexed excipulum (*M. lignaria*). **E**, stipitate (forms of *M. lignaria*). Scale = approx. 200 μm.

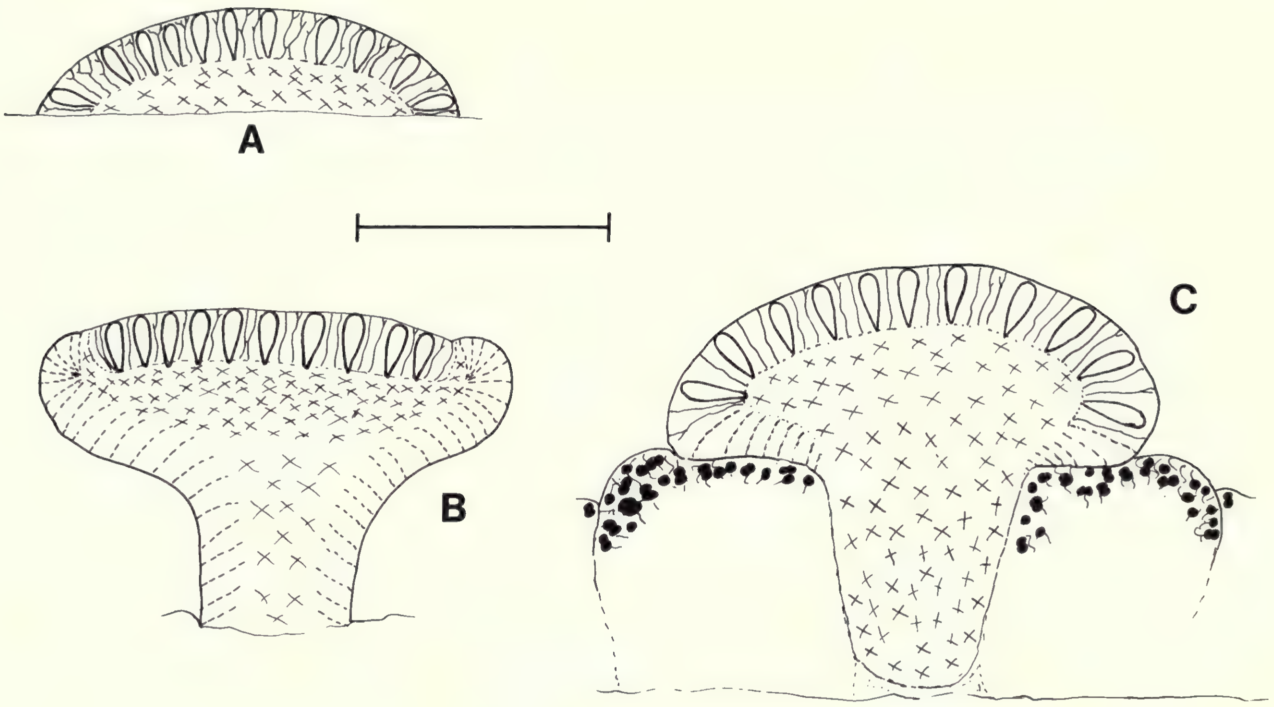


Fig. 4 Some apothecium types in *Micarea* (semi-diagrammatic). **A**, convex and adnate, without excipulum (*M. lithinella.*) **B**, stipitate with well-developed excipulum (*M. crassipes*). **C**, convex with 'rooting' hypothecium (some forms of *M. incrassata*). Scale = approx. 200 μm.

other extreme those of *M. contexta, M. eximia*, and *M. myriocarpa* are ± globose from the beginning and often tuberculate. The range of variability for most other species falls somewhere between these last two extremes. Apothecia are usually sessile (or partly hidden by adjoining areolae or goniocysts) but occasionally, as with *M. lignaria, M. botryoides*, and *M. ternaria*, they may be turbinate or short-stalked (due to vertical elongation of excipular and (or) hypothecial tissues), but only in *M. crassipes* and an undescribed species from New Zealand is this a constant feature (Figs 3E, 4B). Apothecia are usually immarginate, but in those species with a well differentiated excipulum (e.g. *M. cinerea, M. denigrata, M. muhrii, M. peliocarpa*, and *M. ternaria*), a faint marginal zone is sometimes apparent, especially in young apothecia. This zone is rarely raised above the level of the disc, but it is often paler in colour (especially when wet) and slightly more glossy. Even in *M. crassipes*, the only species whose apothecia regularly exhibit a distinctly raised marginal rim, this feature is soon occluded as the disc expands and becomes convex.

The dimensions of apothecia in *Micarea* fall mainly within the range 0·1–0·6 mm diam. In some species (e.g. *M. denigrata, M. peliocarpa*, and *M. prasina*) there is considerable variation in apothecial size, but in others it may be less so. Characteristically small apothecia (<0·3 mm diam) are found in, for example, *M. contexta, M. eximia, M. melaeniza, M. misella, M. myriocarpa*, and *M. rhabdogena*. Species often with large apothecia, sometimes growing to a diameter of 0·7 mm (or even up to 1 mm), include *M. assimilata, M. cinerea, M. incrassata*, and *M. ternaria*. These dimensions relate to 'normal' convex to globose apothecia; however, larger sizes are often attained when the apothecia become tuberculate (Fig. 3C). The apothecia of *M. tuberculata* are usually less than 0·3 mm diam, but when tuberculate may reach 0·5 mm diam. Some other examples with equivalent dimensions are: *M. anterior* (0·3 mm, 0·6 mm), *M. bauschiana* (0·4 mm, 0·7 mm), *M. botryoides* (0·25 mm, 0·5 mm), *M. cinerea* (0·7 mm, 1·3 mm), *M. elachista* (0·3 mm, 0·8 mm), *M. lutulata* (0·4 mm, 0·8 mm), and *M. sylvicola* (0·5 mm, 1·2 mm). The apothecia of *M. adnata* are nominally *c.* 0·2–0·4 mm diam but they often coalesce and become somewhat tuberculate, producing large nodulose clusters up to about 2 mm across.

The apothecia of certain species (*M. adnata, M. alabastrites, M. pycnidiophora*, and *M. stipitata*) are always devoid of pigments and hence whitish or pallid in colour and ± translucent when wet. Conversely, those of certain other species are heavily pigmented and invariably blackish and opaque when wet (e.g. *M. assimilata, M. contexta, M. crassipes, M. eximia, M. incrassata, M. intrusa, M. melaena, M. melaenida, M. melaeniza, M. nigella, M. olivacea, M. subviolascens*, and *M. ternaria*). Black apothecia are also characteristic of *M. lignaria, M. misella*, and *M. turfosa*, but bluish grey or brown shade-forms have been encountered. The apothecia of a number of species (notably *M. bauschiana, M. denigrata, M. peliocarpa*, and *M. prasina*) commonly occur as forms ranging from whitish or pallid, to blue-grey or pale-brown (sometimes white/blue-grey or white/brownish piebald), through dark grey or dark brownish grey, to black. The consequent array of colour forms, combined with much variability with regard to size and shape of apothecia, thallus development and substrata, has resulted in a large synonymy for each of these species! In such variable species apothecial colour is largely dependent on the light regime experienced by individual apothecia. This can be demonstrated in the field by observing the species in situations where large changes in light intensities occur over short distances (a few centimetres or less). Such a situation is portrayed in Fig. 5, by an example of *M. bauschiana* growing all over the exposed parts of a flat stone lodged in the dry underhang of a bank, alongside a woodland road.

Species such as *M. curvata, M. elachista, M. myriocarpa, M. osloensis*, and *M. subnigrata* have brown or brown-black apothecia due to the presence of a brown epithecial pigment. The external brownish colour may also result from the combination of a colourless (or ± so) hymenium and epithecium and a dark brown hypothecium (e.g. in forms of *M. lutulata* and *M. muhrii*). However, brown apothecia as sometimes encountered in, for example, *M. bauschiana* and *M. denigrata*, often indicate the presence of a dematiaceous hyphomycete (? *Bispora* sp.) parasitizing the apothecial tissues. Apothecia which appear blue-grey or blue-black contain a green (K−) epithecial or hymenial pigment (e.g. in *M. bauschiana, M. peliocarpa*, and *M. sylvicola*), or similarly located high concentrations of the olivaceous (K+ violet) pigment (e.g. in

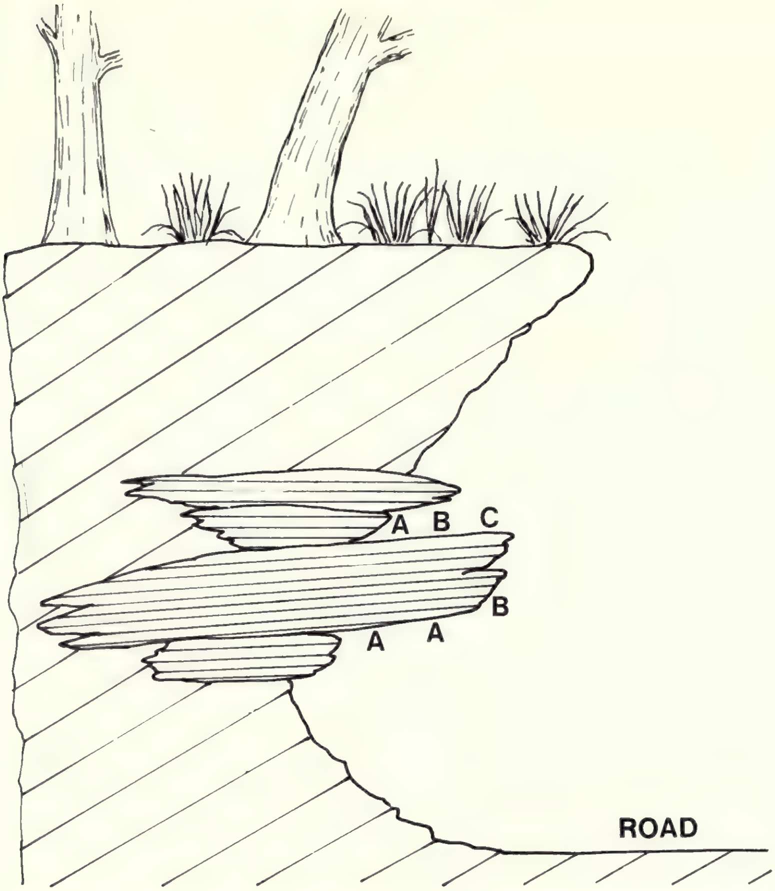


Fig. 5 Sketch demonstrating a situation which *M. bauschiana* shows variation in the colour of its apothecia, from pallid (A), through pallid/brownish or pallid/blue-grey (B), to blue-black (C). Site: roadside bank in woodland in lower Glen Roy, Westerness (cf. *Coppins* 3492/3, E); the bank is *c.* 1 m high).

M. denigrata, M. nitschkeana, and *M. prasina*. I know of no *Micarea* that has apothecia possessing pruina or, exhibiting a bluish (caesious) 'bloom' when wetted. Such features are due to the existence in the epithecium of minute colourless (or pale straw when dense) granules that dissolve in K, and are characteristic of several species often misidentified to *Micarea*, e.g. *Bacidia beckhausii, Lecanora symmicta* agg., *Lecidea caesioatra, L. turgidula*, and *Scoliciosporum pruinosum*.

Apothecia: internal features

All tissues of the apothecia are bound by a weak gel-matrix which ± dissipiates in 10% KOH to clearly reveal the component parts (i.e. hyphae, paraphyses, and asci). In some species the apices of the paraphyses and/or the hyphae of the hypothecium are additionally cemented by dense pigment deposited in the matrix and/or on the hyphal walls, thus tending to impair their separation in K. The presence of the gel-matrix serves to separate species of *Micarea* from some superficially similar species of *Vezdaea* (Poelt & Döbbeler, 1975).

Hymenium and epithecium

The term 'epithecium' is here employed in its broad sense to refer to the upper part (usually *c.* 3–15 μm) of the hymenium where this differs in appearance from the remaining lower part(s).

This difference can be due to the much branched and entangled apices of the paraphyses, or (and) deposits of pigment in the gel-matrix, or on (or in) the walls of the paraphyses. The upper layer of the hymenium differentiated in such ways is perhaps more correctly termed the 'epihymenium' (Poelt, 1974*a*) or 'pseudoepithecium' (Korf, 1973). In its strict (original) sense an 'epithecium' refers to a layer of branches of paraphyses that overtop the asci. Such a layer is approached in some species of *Micarea* and is best exemplified by *M. contexta* and *M. melanobola*. In *Micarea* the difference between an 'epihymenium' and an 'epithecium' is not clear-cut, and so I have chosen to employ the latter term which has been long and widely employed in lichenology.

The height of the hymenium in *Micarea* species is sometimes difficult to measure accurately because the hymenium often merges rather imperceptibly into the hypothecium. Measurements are most accurately made by mounting thin sections in Lugol's iodine, in which the strongly amyloid (dark blue) hymenium contrasts strongly with the non-amyloid (or ± so) hypothecium. Even when accurately determined the height of the hymenium is rarely a useful character in distinguishing similar species. The overall range in height is about 23–90 μm, and in most cases is within 35–50 μm. Shallow hymenia (rarely exceeding 35 μm) are characteristic of many of the species with small spores, viz.: *M. hedlundii, M. melanobola, M. misella, M. myriocarpa, M. nigella, M. olivacea, M. osloensis, M. rhabdogena,* and *M. tuberculata*. Likewise, tall hymenia are characteristic of species with large spores, and the tallest hymenium (65–90 μm) belongs to the species with the largest spores, namely *M. subleprosula*. The height of the hymenium sometimes increases with the age of the apothecium, and this is particularly true in *M. bauschiana* and *M. sylvicola*: small, yet mature, apothecia usually have a hymenium *c.* 40 μm tall, but as the apothecium enlarges and increases in convexity, the hymenium often increases in height up to about 60 μm; at the same time the paraphyses appear to 'stretch' and become thinner (especially in the lower part of the hymenium).

The hymenium in *Micarea* never contains hyaline, crystalline inclusions that adhere to paraphyses (as found in some species of *Lecidella*, and many *Graphidaceae*) or numerous oil droplets (as found in several species of *Buellia* and *Caloplaca*). Epithecial granules that dissolve in K and often give the apothecia a pruinose appearance are also never found in *Micarea*. Minute granules of blue-violet (K+aeruginose) pigment, like those found in *Lecidea hypnorum*, are occasionally observed in the hymenium of *M. contexta* and *M. lignaria*.

The colour of the hymenium and epithecium is an important character in the identification of *Micarea* species. A discussion of the various pigments involved is given in the sections on 'chemistry'. The hymenium may be dilutely and ± evenly coloured throughout, or the colouration may be more intense in the upper part. In many species the hymenium is often intersected by dark vertical streaks, a feature usually due to dense pigment surrounding individual, or small fascicles of stout paraphyses (see p. 61).

Asci

The asci of *Micarea* species are clavate or cylindrical-clavate in shape and belong to the *Lecanora*-type of Honegger (1978). When mounted in Lugol's iodine (following treatment in 10% KOH) the ascus is seen to have a non-amyloid wall surrounded by an amyloid outer-layer ('fuzzy coat') and an internal staining amyloid apical dome (Fig. 6). *Micarea* has sometimes been placed in the *Arthoniaceae* (e.g. Lamb, 1953) but the ascus of members of that family does not have an amyloid outer-layer and the apical dome is not deeply amyloid. In a few species of *Arthonia* and *Arthothelium* I have observed a faint bluing in the part of the apical dome immediately adjacent to the ocular chamber. In some *Arthonia* species a tiny amyloid ring is apparent above the apex of the ocular chamber, and, despite statements to the contrary by Eriksson (1981), such a ring *is* found in the asci of *A. radiata* (type species of *Arthonia* Ach.) and *A. fuscopurpurea*. The same type of ring was also described for *Bryostigma leucodontis* by Poelt & Döbbeler (1979). Such aspects of ascus structure in the *Arthoniaceae* clearly merit more detailed investigation. The ascus structure in *Micarea* supports my opinion that the genus should be placed in the *Lecideaceae s. str.*, at least for the time being.

The asci of all European *Micarea* species are 8-spored. The North American *Lecidea populina*

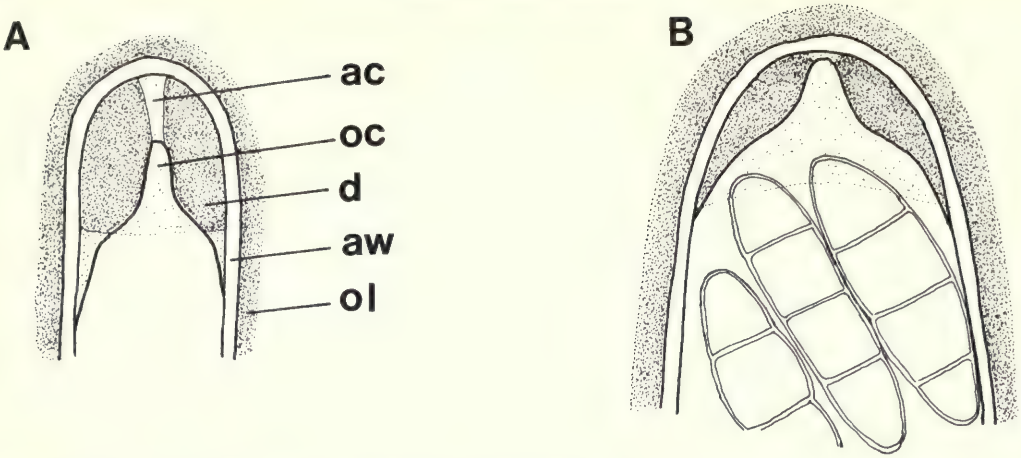


Fig. 6 Ascus apex of *Micarea alabastrites* in optical section (LM); mounted in Lugol's iodine following pre-treatment in 10% KOH. **A**, young ascus. **B**, mature ascus. ac, apical cushion; aw, ascus wall; d, apical dome (tholus); oc, ocular chamber; ol, outer layer of ascus wall. Shading indicates intensity of amyloid reaction; note that in reality the apical cushion and ocular chamber are probably completely non-amyloid. Scale = 10 μm.

Müll. Arg. has 16-spored asci and was transferred to *Micarea* by Anderson & Carmer (1974). Unfortunately the type material of *L. populina* has been out on loan from H and not available to me during the course of this study. However, the species apparently occurs in *Xanthorion* communities and, if this is so, then it is unlikely to be a *Micarea*.

Spores

The wide variety of spore types found in *Micarea* can be seen in the selection of spores from all the European species illustrated in Figs 7–33. A few species (e.g. *M. assimilata, M. contexta,* and *M. lithinella*) have spores that are ± consistent in size, shape, and septation, but for many other species (e.g. *M. anterior, M. botryoides, M. denigrata, M. prasina*, and *M. turfosa*) these characters can be very variable even within the same ascus. The smallest spores are found in *M. myriocarpa* (5·5–8·5×1·5–2·5 μm) and the largest ones are found in *M. subleprosula* (40–60× 5–6·6 μm). Spores may be simple or up to 7-septate, the variations within these limits depending on the species. Spores with more than 7-septa are very rare, although a few 9-septate spores have been observed in *M. subleprosula*, and a collection (Coppins, 1834) of *M. synotheoides* has spores with up to 11 septa. Among the great range of spore shapes encountered, some may be broadly ellipsoid (*M. subnigrata* and *M. intrusa*), but regularly globose spores do not occur in *Micarea*.

Healthy spores are always thin-walled and colourless. However, the walls of old spores trapped within the hymenium sometimes become slightly thickened and pale straw coloured, or they may become impregnated with hymenial pigment. Spore walls always appear smooth (LM at ×1000) and are never surrounded by a gelatinous epispore. The cytoplasm of spores, asci, and ascogenous hyphae in *M. intrusa* is sometimes a dilute orange, turning purple-red in K.

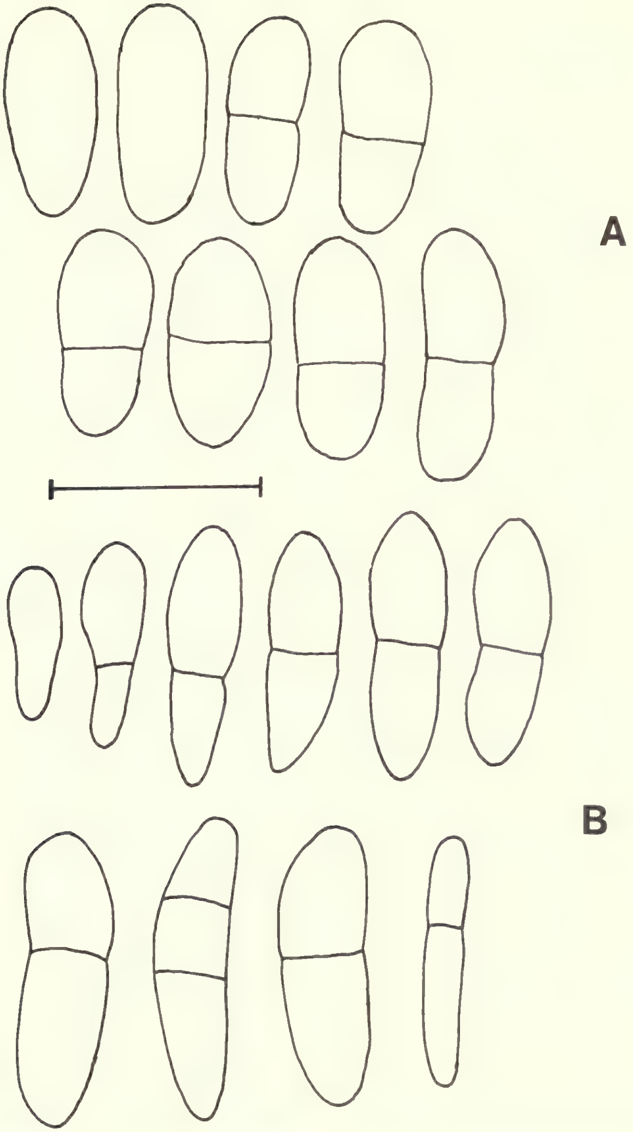


Fig. 7 **A**, *M. adnata* (E – holotype). **B**, *M. anterior* (H-NYL 21655 – lectotype). Scale = 10 μm.

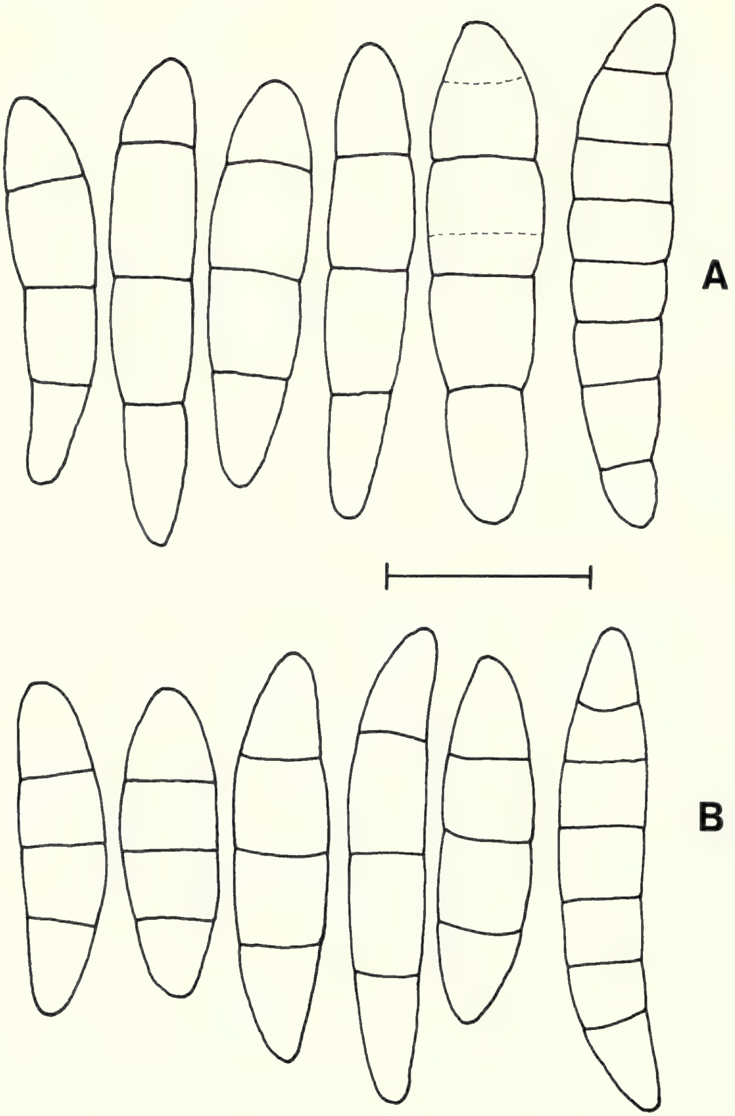


Fig. 8 *M. alabastrites*. **A**, (H-NYL 18656 – holotype). **B**, (*Coppins* 2588, E). Scale = 10 μm.

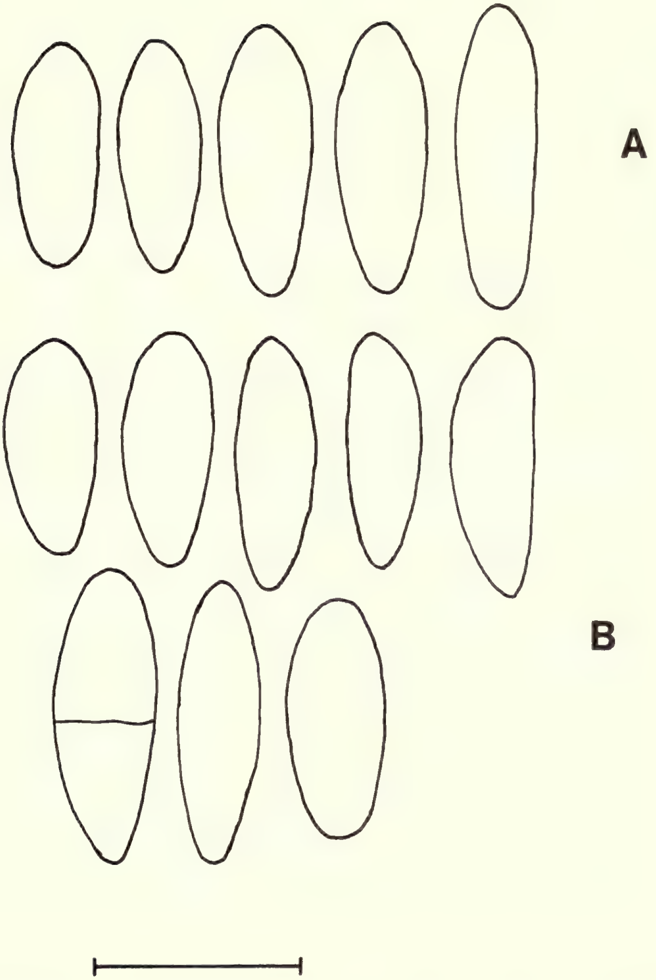


Fig. 9 *M. assimilata*. **A**, (H-NYL 16556 – lectotype). **B**, (Norway, Oppland, Fogstuen, 1857, *Lindsay*, E). Scale = 10 μm.

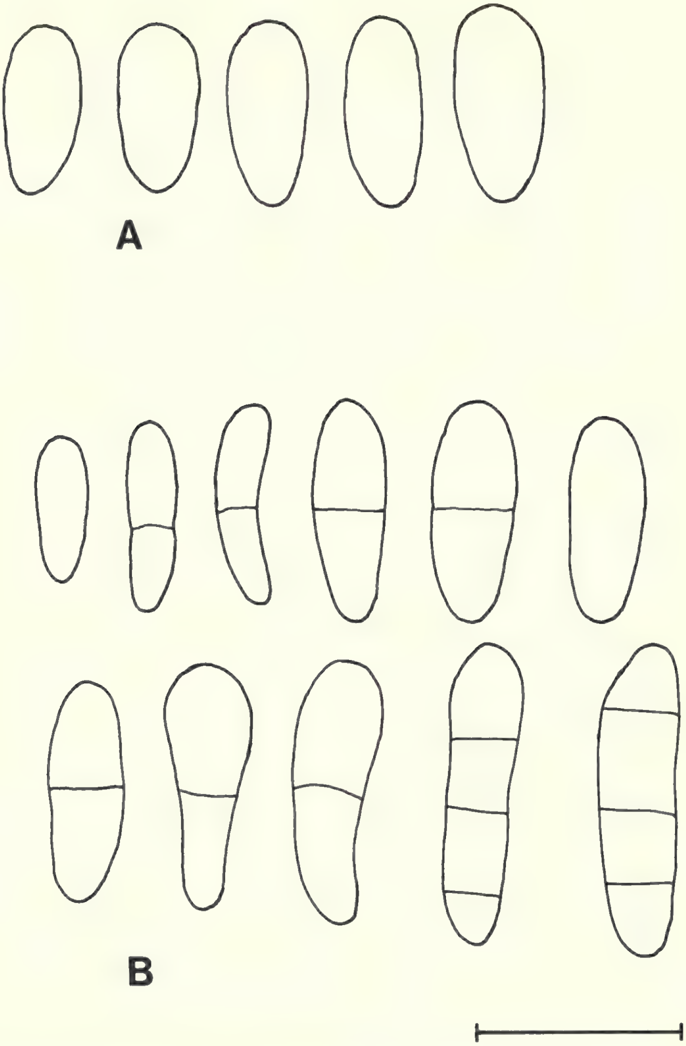


Fig. 10 **A**, *M. bauschiana* (M – lectotype). **B**, *M. botryoides* (*Coppins* 8429, E). Scale = 10 μm.

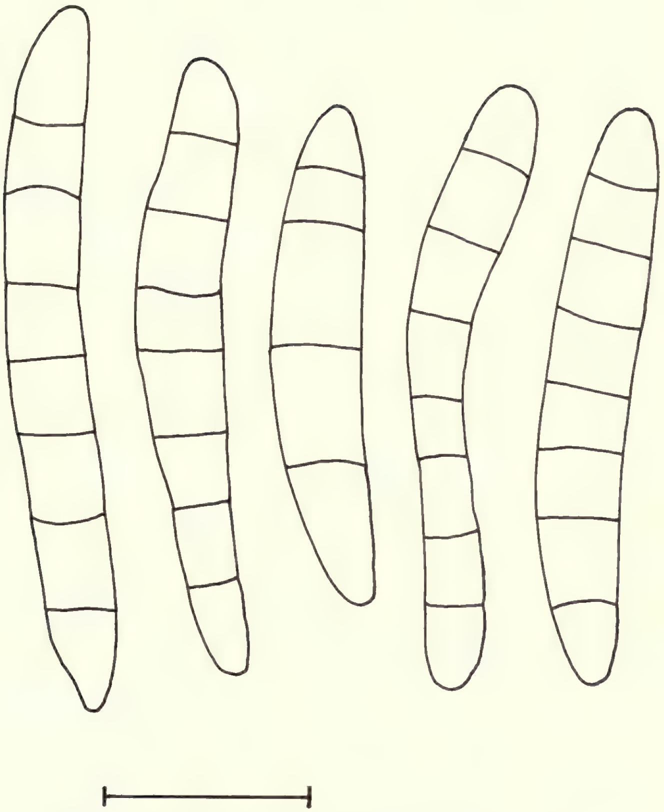


Fig. 11 *M. cinerea* (*Coppins* 2533, E). Scale = 10 μm.

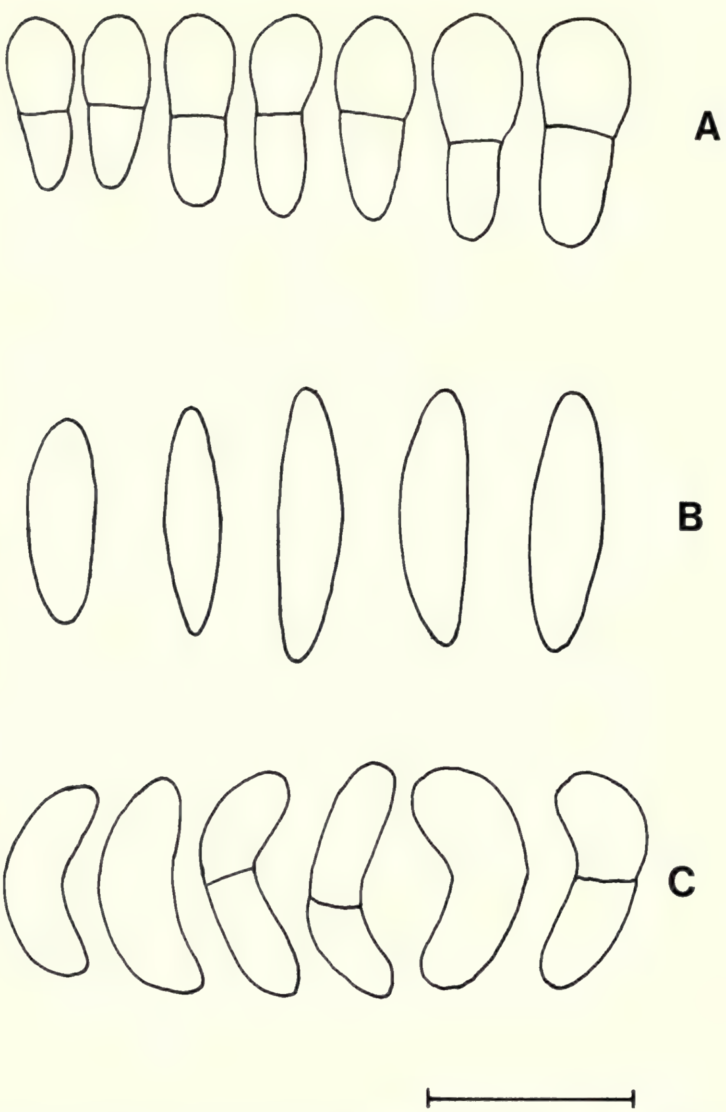


Fig. 12 **A**, *M. contexta* (S – lectotype). **B**, *M. crassipes* (Vězda Lich. Sel. 11, BM). **C**, *M. curvata* (WRSL – holotype). Scale = 10 μm.

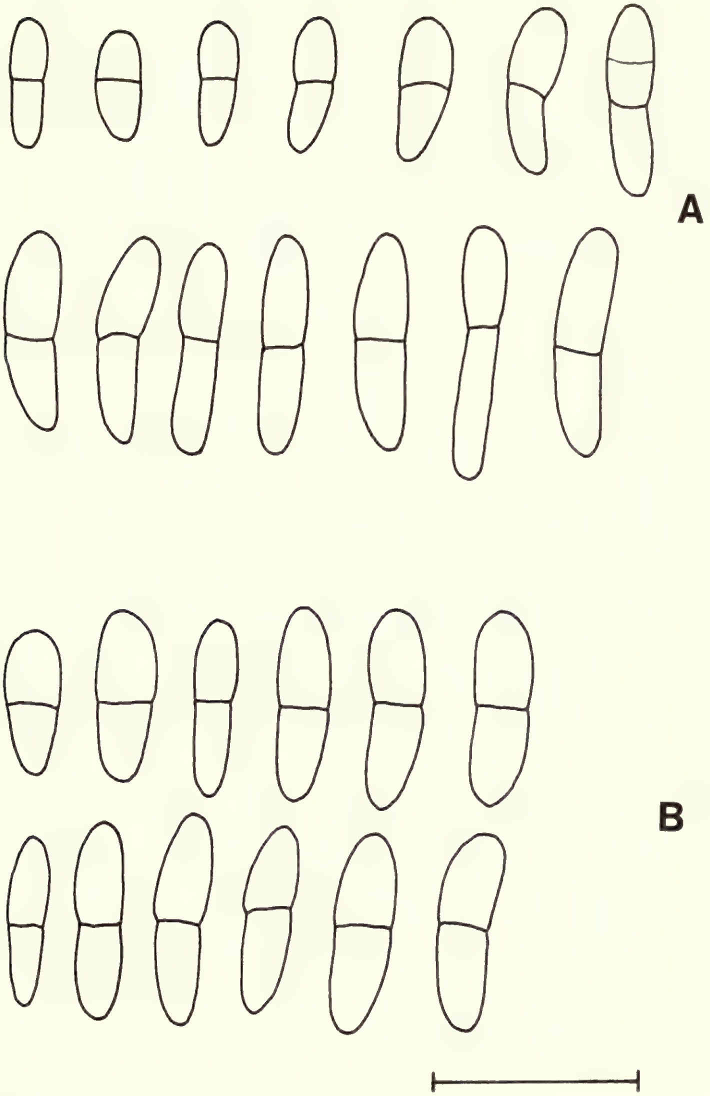


Fig. 13 *M. denigrata.* **A**, (UPS – lectotype). **B**, (H – lectotype of *Lecidea hemipoliella*). Scale = 10 μm.

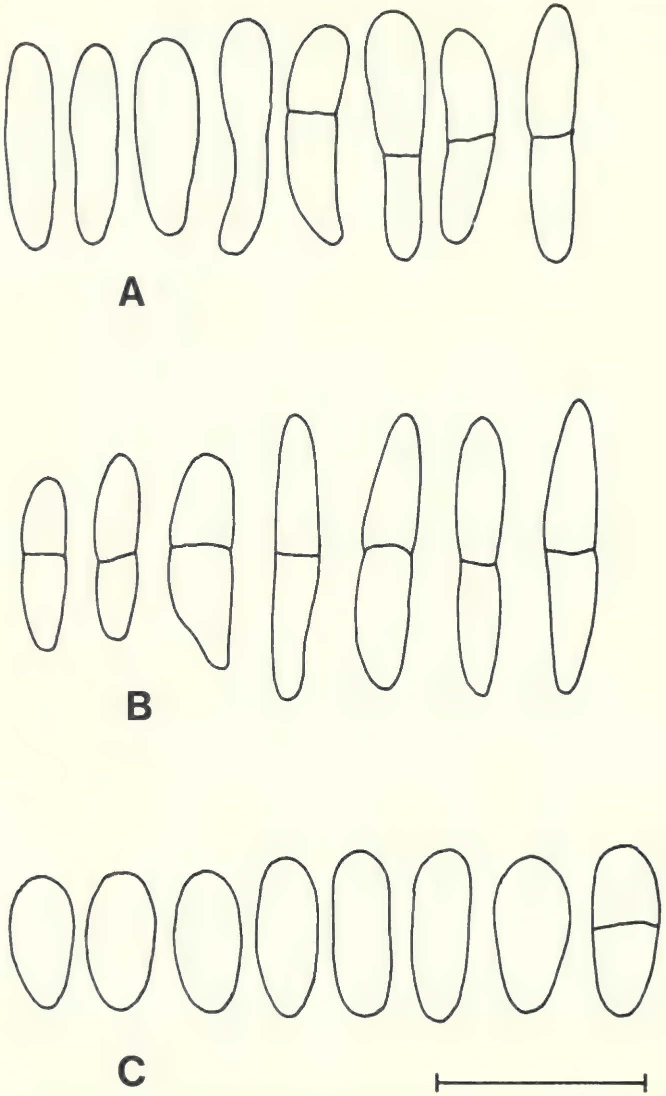


Fig. 14 **A**, *M. elachista* (L – lectotype). **B**, *M. eximia* (S – lectotype). **C**, *M. hedlundii* (UPS – holotype). Scale = 10 μm.

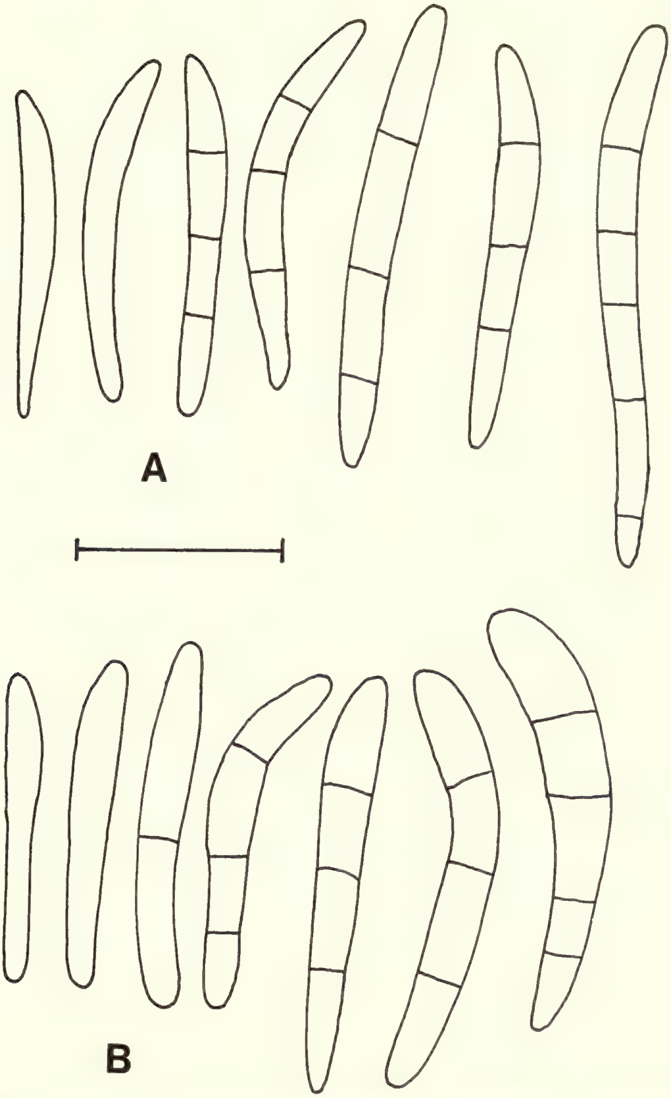


Fig. 15 *M. globulosella.* **A**, (S – lectotype). **B**, (Czechoslovakia, Slovakia, Vysoké Tatry, 1879, *Lojka*, BM). Scale = 10 μm.

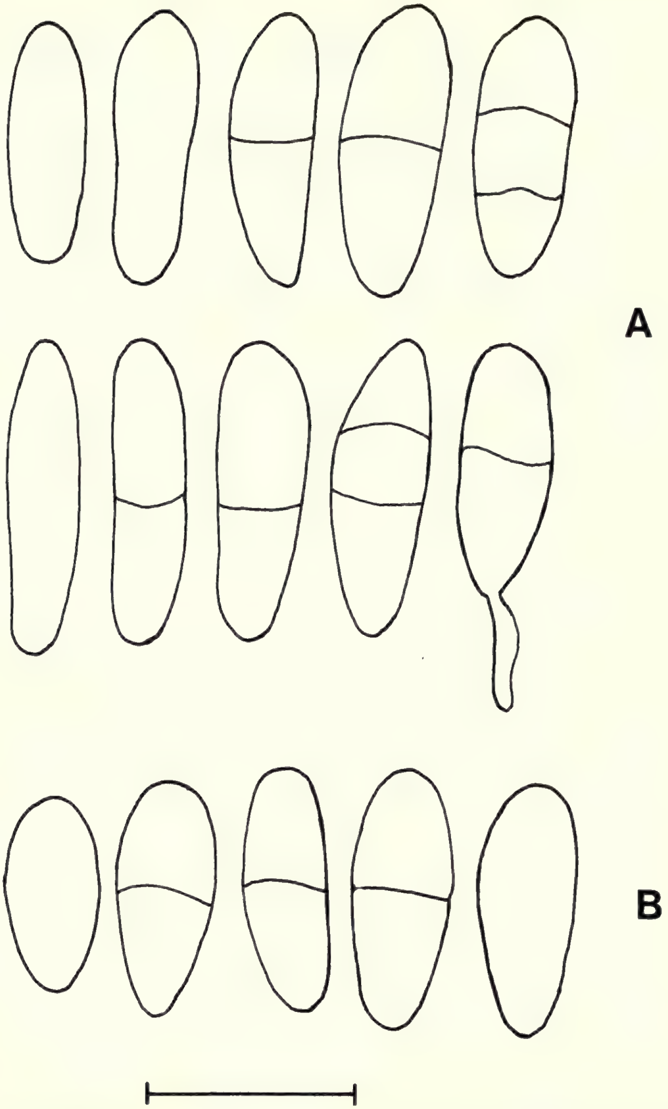


Fig. 16 *M. incrassata.* **A**, (S – holotype). **B**, (Kerguelen, 1875, *Eaton*, E). Scale = 10 μm.

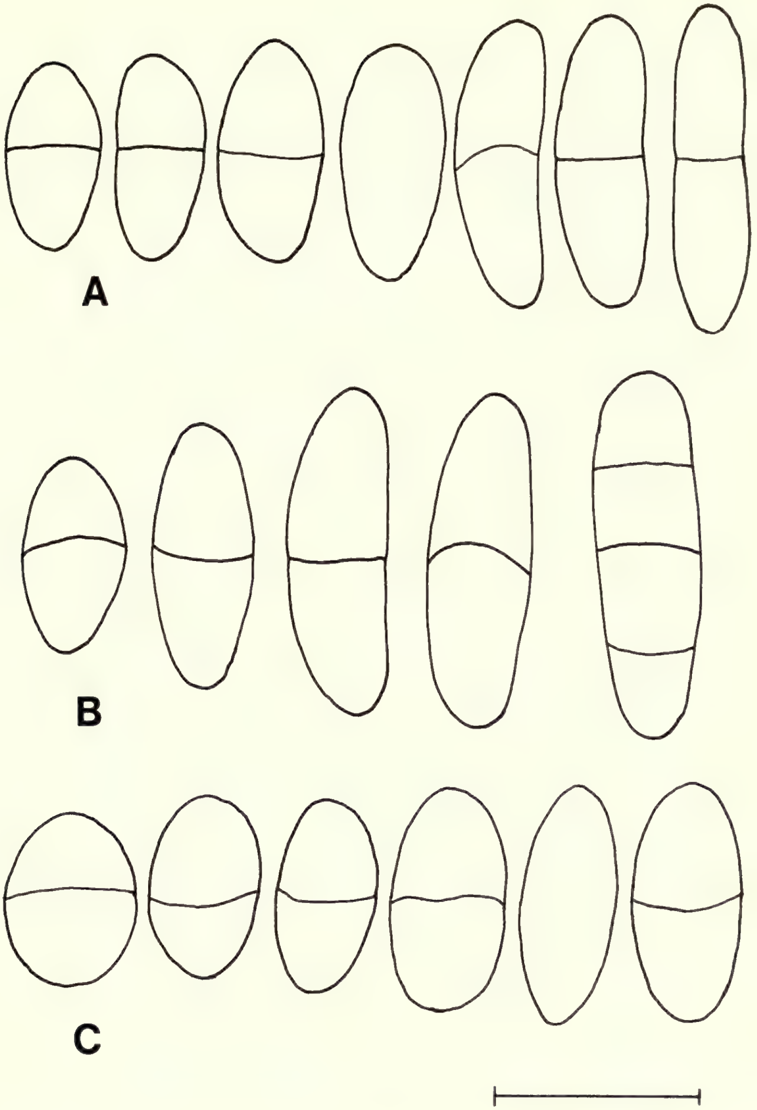


Fig. 17 *M. intrusa.* **A**, (UPS – holotype). **B**, (BM – isotype of *Lecidea melaphana*). **C**, (Norway, Hordaland, Fjell, 1980, *Skjolddal,* BG). Scale = 10 μm.

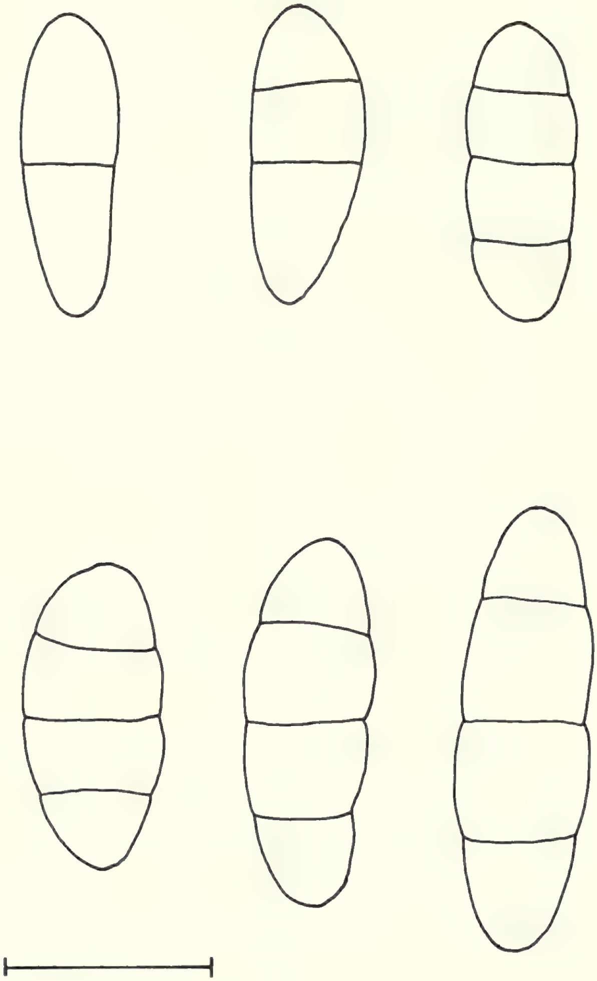


Fig. 18 *M. leprosula* (UPS – lectotype). Scale = 10 μm.

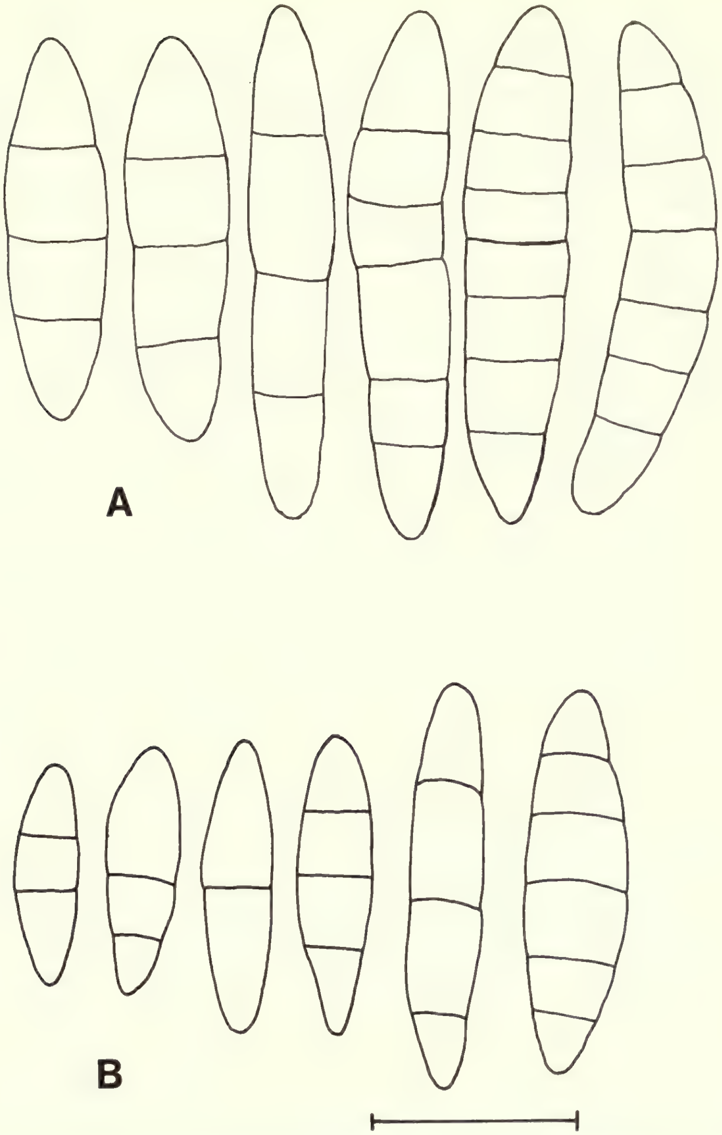


Fig. 19 *M. lignaria.* **A**, (H-ACH 265 – lectotype). **B**, (TUR-VAINIO 21274 – lectotype of *Lecidea trisepta* var. *polytropoides*). Scale = 10 μm.

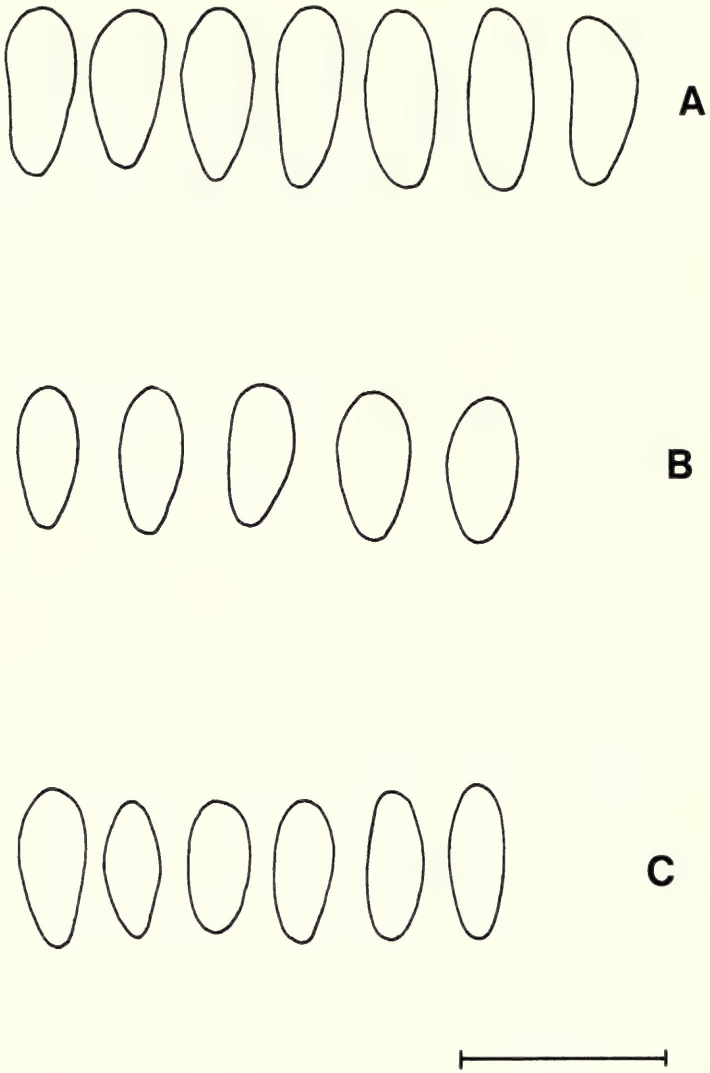


Fig. 20 **A–B**, *M. lithinella*; **A**, (M – lectotype); **B**, (Germany, Heidelberg, *Zwáckh*, H-NYL 19191). **C**, *M. lutulata* (Wales, Pembroke, Tycanol, 1980, *James*, BM). Scale = 10 μm.

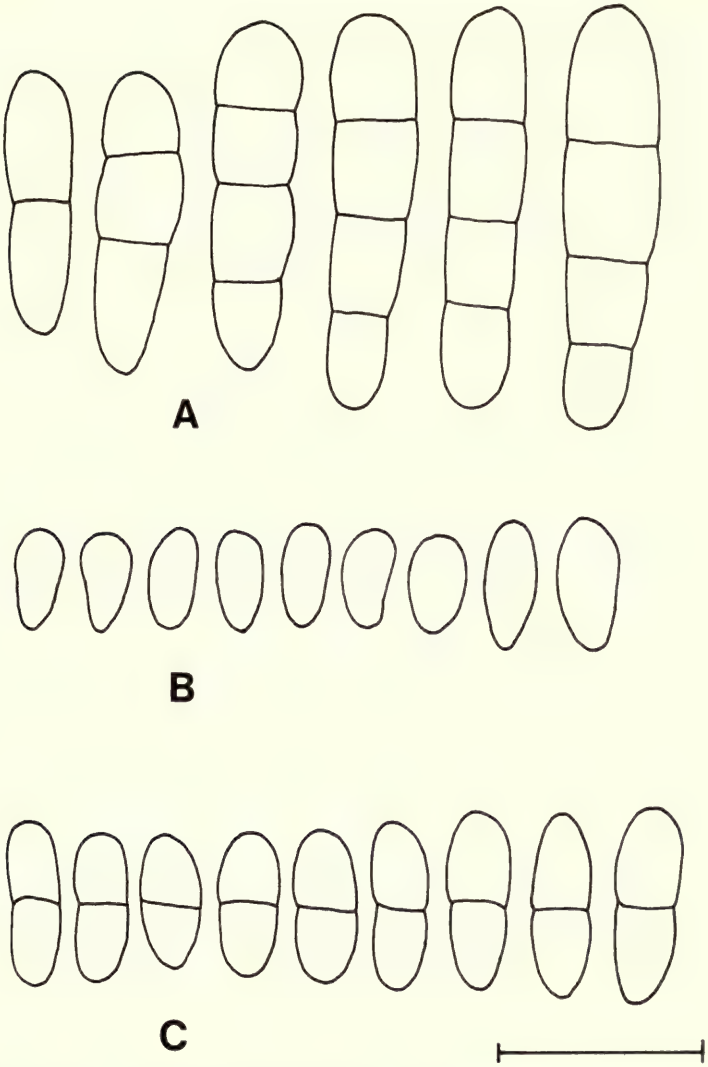


Fig. 21 **A**, *M. melaena* (UPS – lectotype of *Lecidea milliaria* var. *turfosa*). **B**, *M. melaeniza* (S – holotype). **C**, *M. melanobola* (H-NYL 21614 – lectotype). Scale = 10 μm.

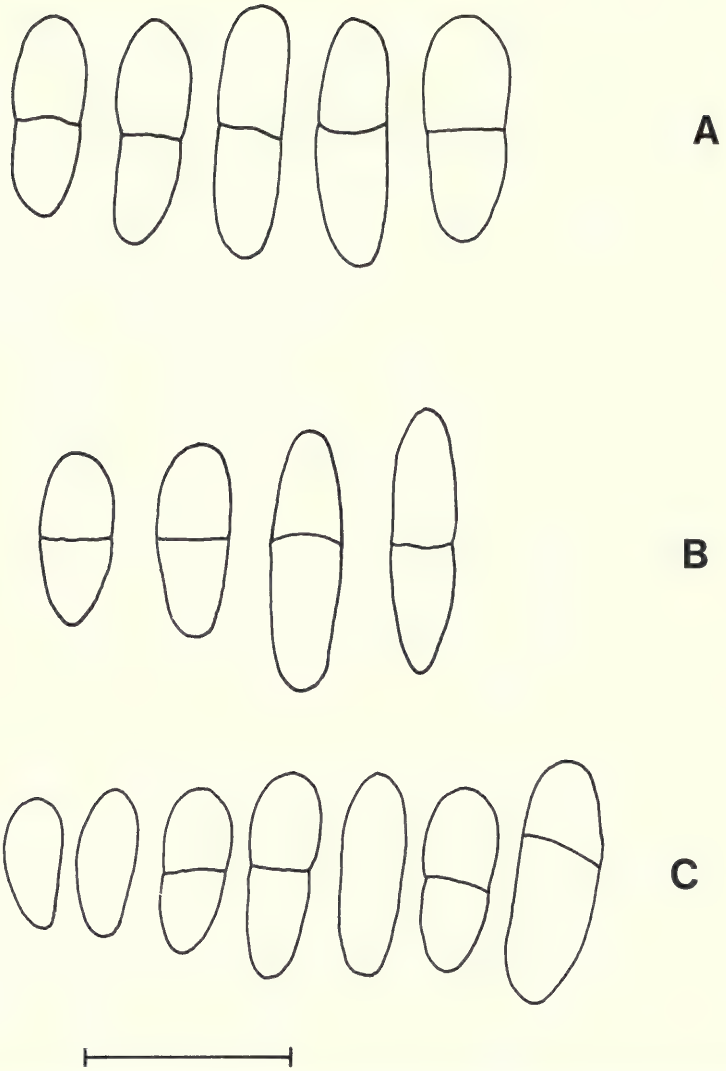


Fig. 22 *M. melaenida*. **A**, (H-NYL 18843 – holotype). **B**, (Fl. Hung. exs. 714, BM – topotype of *Catillaria zsakii*). **C**, (WRSL – lectotype of *Catillaria schumanii*). Scale = 10 μm.

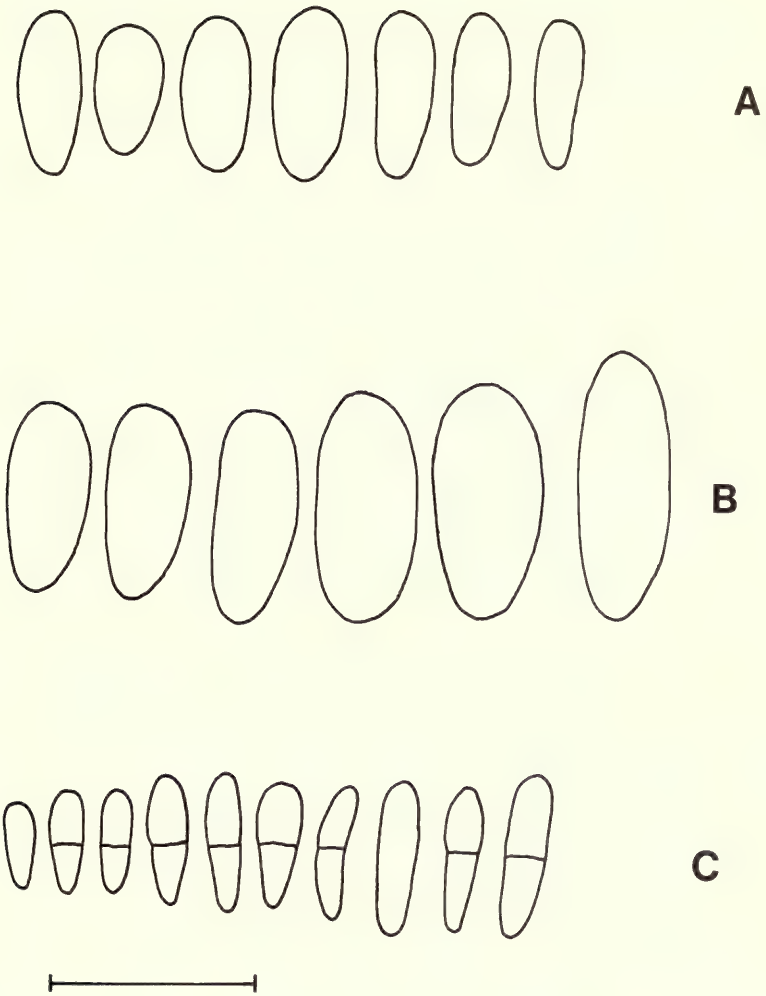


Fig. 23 **A**, *M. misella* (H-ACH 52-holotype of *Lecidea resinae* subsp. *globularis*). **B**, *M. muhrii* (E – holotype). **C**, *M. myriocarpa* (hb Wirth 6085 – holotype). Scale = 10 μm.

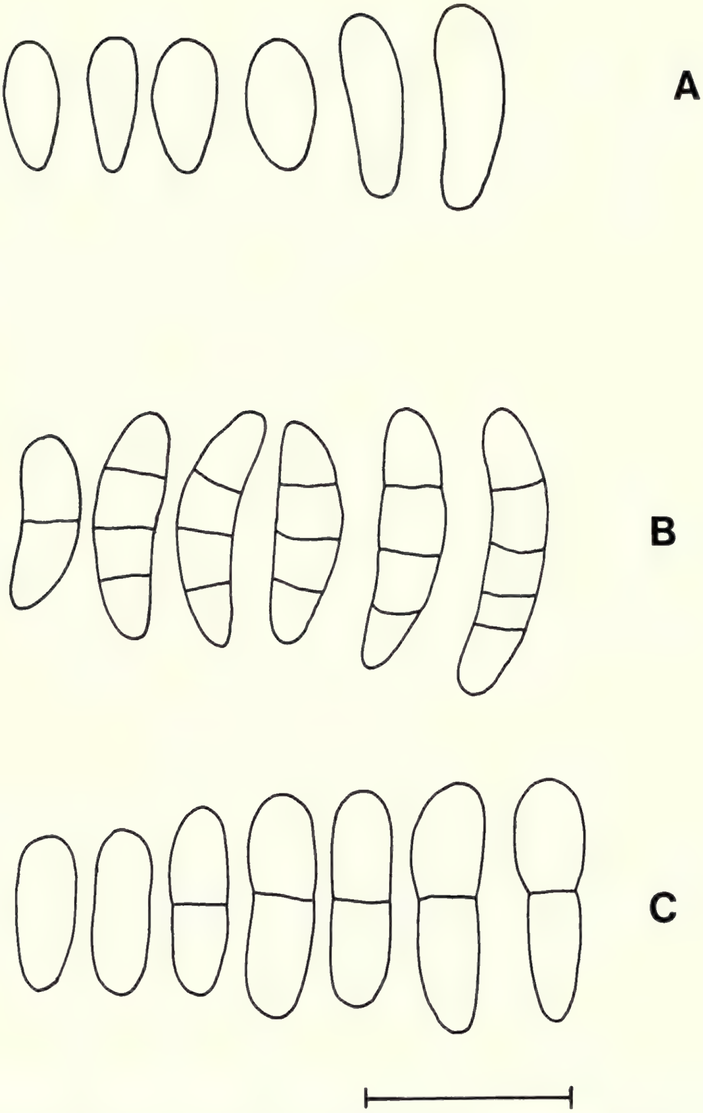


Fig. 24 **A**, *M. nigella* (E – holotype). **B**, *M. nitschkeana* (*Coppins* 2426, E). **C**, *M. olivacea* (BM – holotype). Scale = 10 μm.

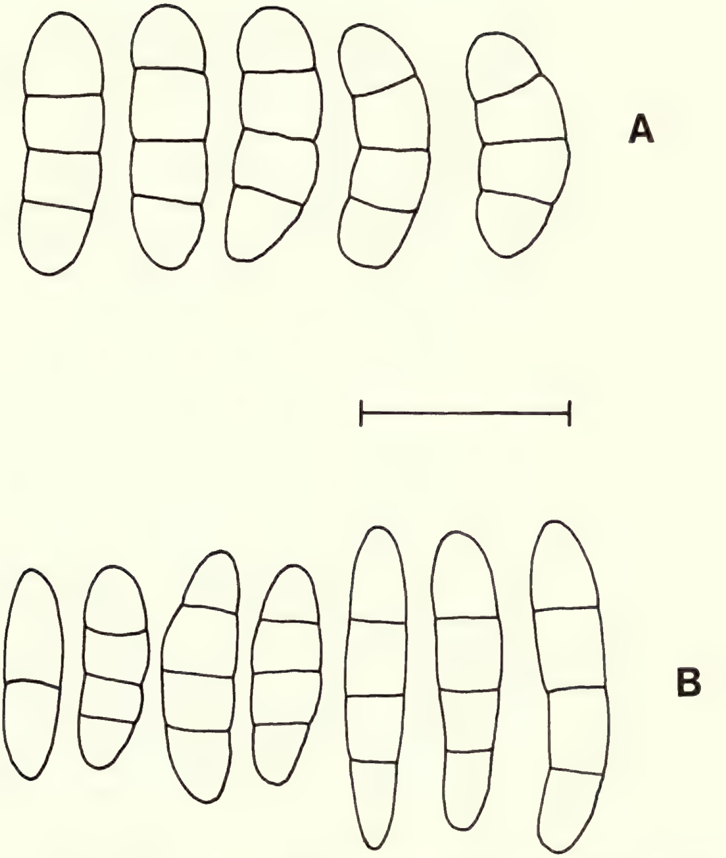


Fig. 25 *M. peliocarpa.* **A**, (H-NYL 18716 – isotype of *Lecidea violacea*). **B**, (England, New Forest, Great Wood, Bramble Hill Walk, 1970, *Coppins et al.*, E). Scale = 10 μm.

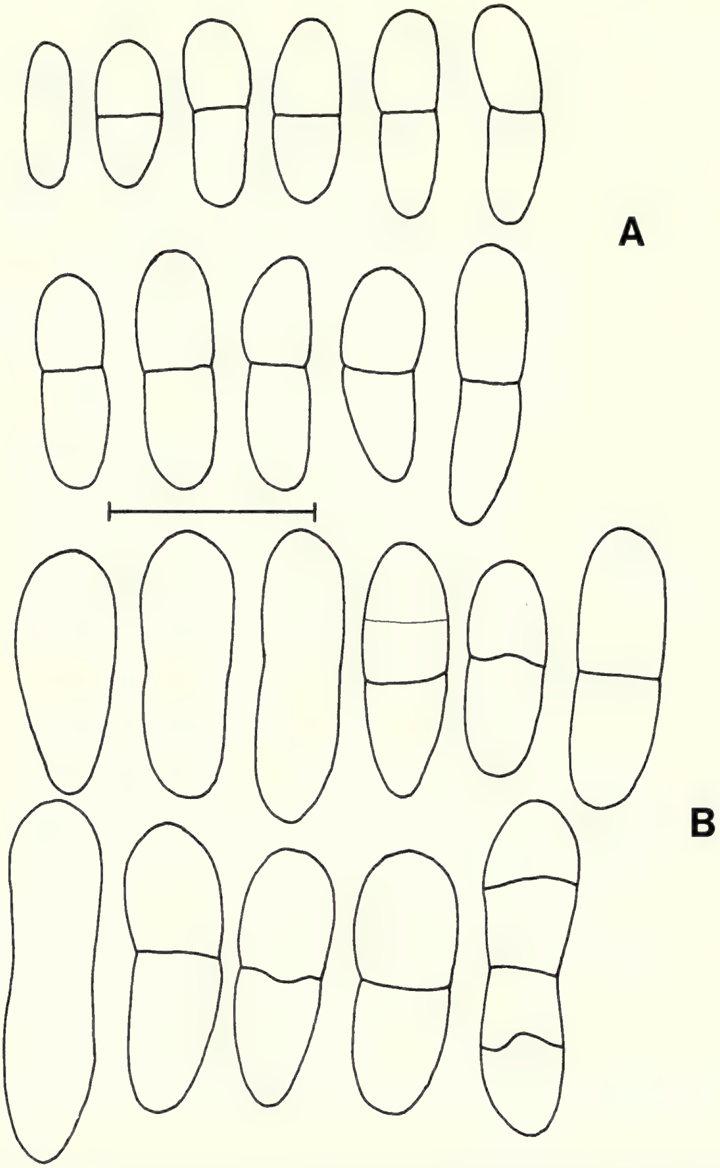


Fig. 26 *M. prasina.* **A**, (UPS – lectotype). **B**, (H-NYL 19056 – lectotype of *Lecidea subviridescens*). Scale = 10 μm.

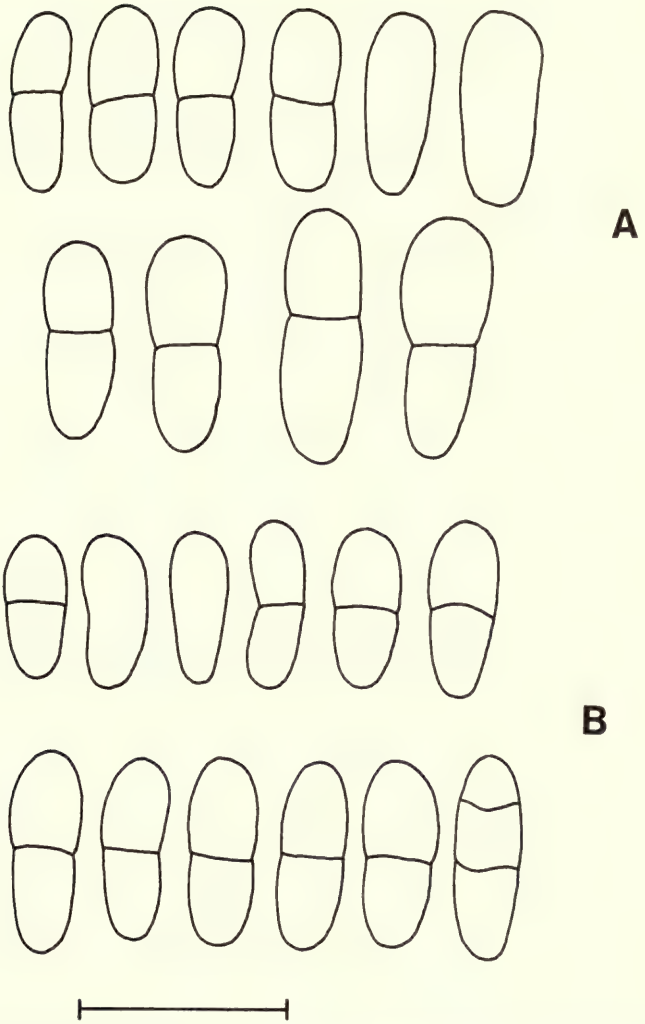


Fig. 27 *M. prasina.* **A**, (H-NYL 21604 – lectotype of *Lecidea prasiniza*). **B**, (GZU – holotype of *Micarea polytrichi*). Scale = 10 μm.

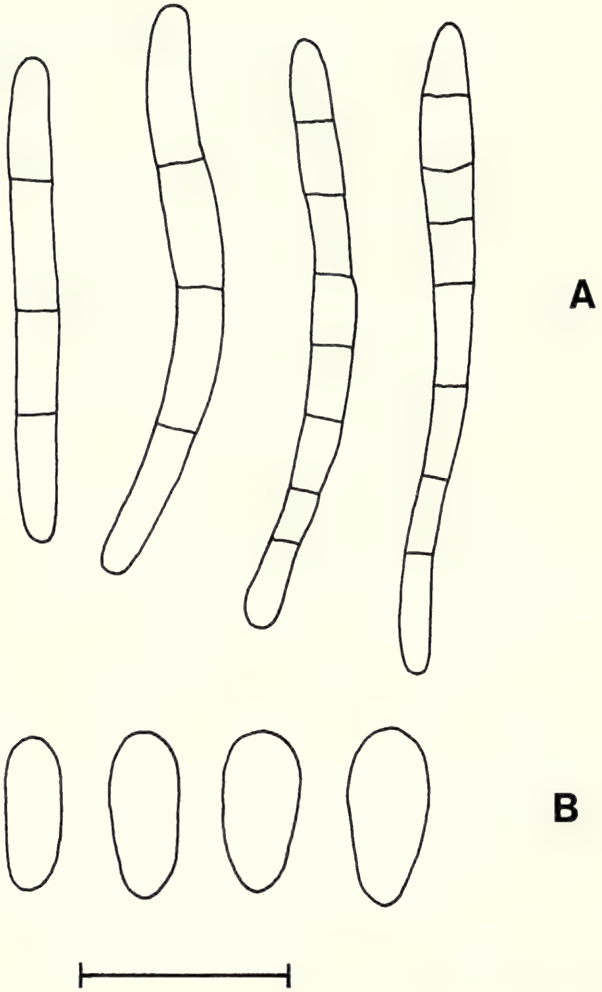


Fig. 28 **A**, *M. pycnidiophora* (E – holotype). **B**, *M. osloensis* (UPS – holotype). Scale = 10 μm.

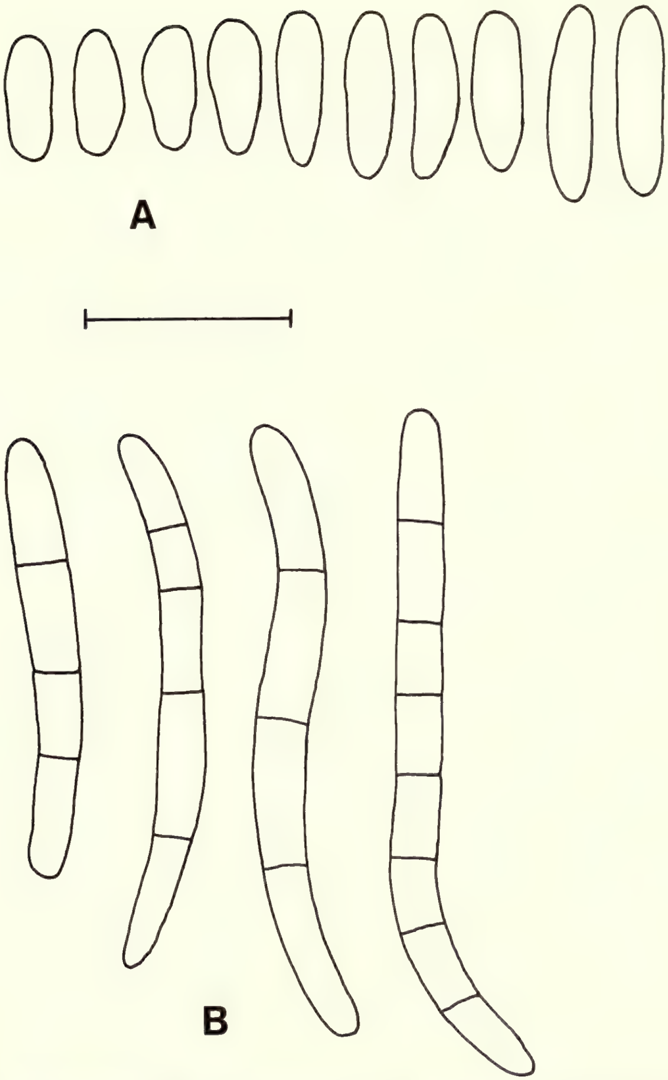


Fig. 29 **A**, *M. rhabdogena* (BM – isolectotype). **B**, *M. stipitata* (E – holotype). Scale = 10 μm.

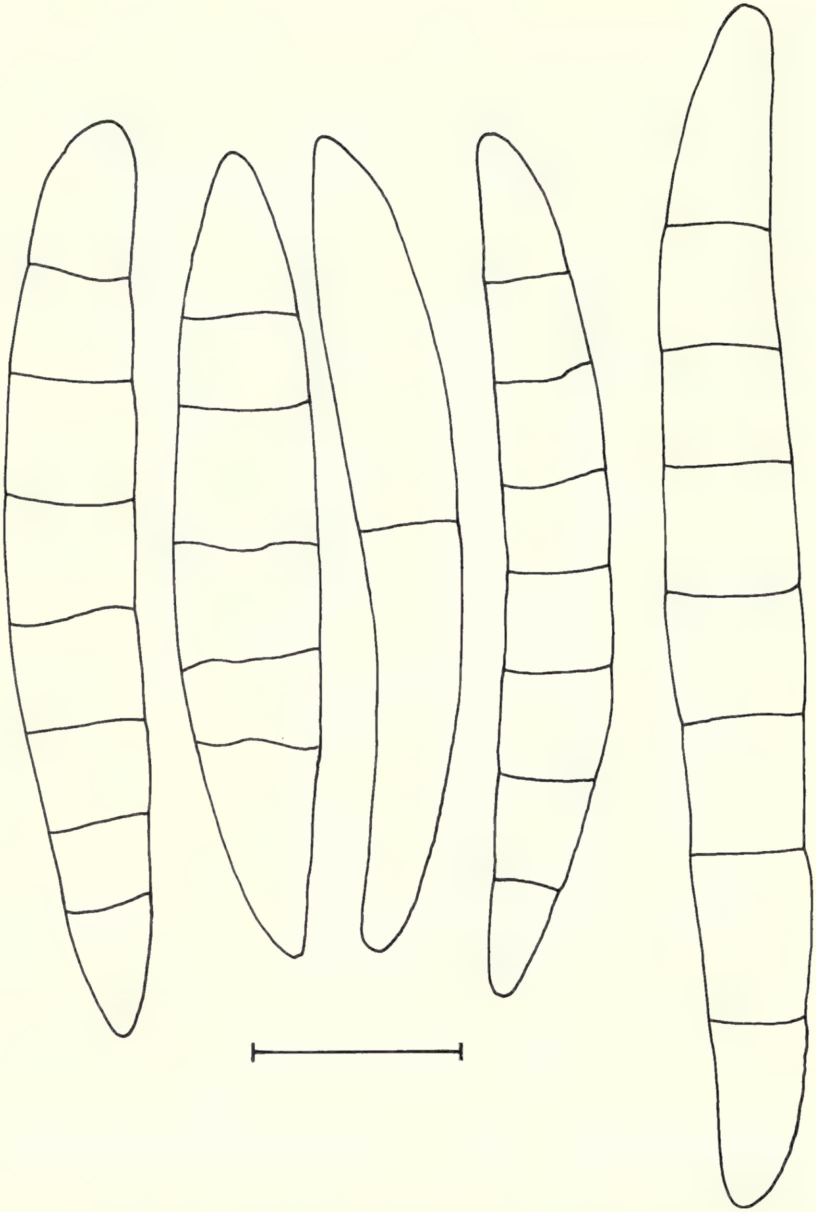


Fig. 30 *M. subleprosula* (*Muhr* 4380, E). Scale = 10 μm.

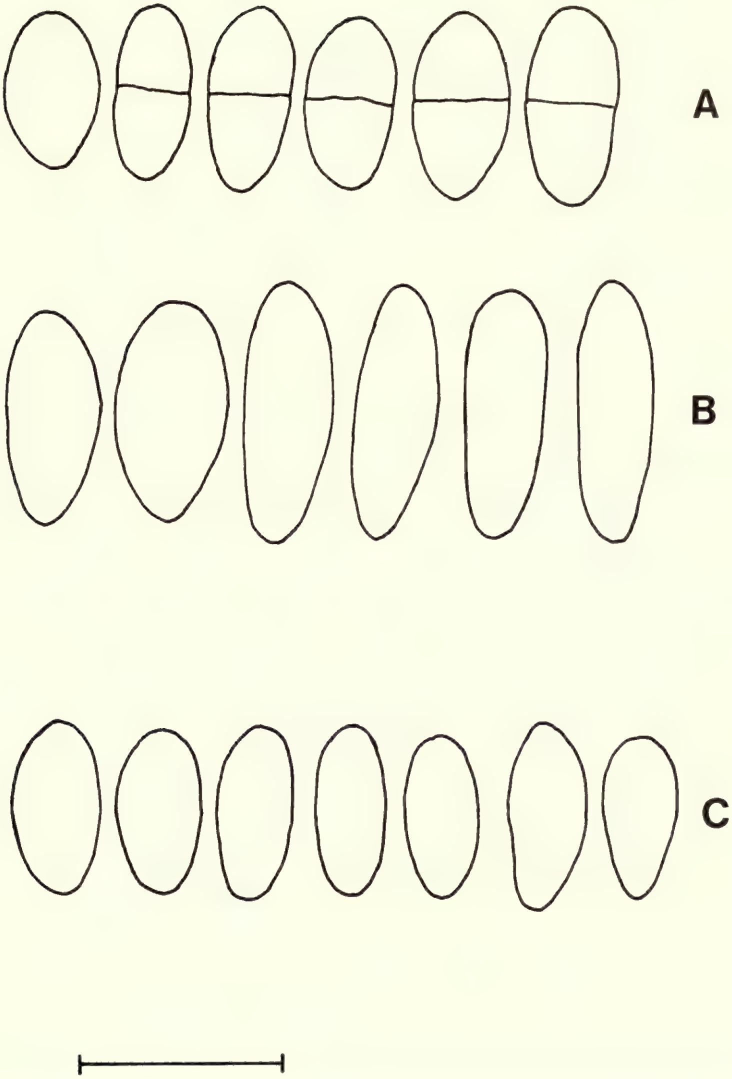


Fig. 31 **A**, *M. subnigrata* (H-NYL 19136 – lectotype). **B**, *M. subviolascens* (Havaas Lich. Exs. Norv. 139, BG). **C**, *M. sylvicola* (UPS – lectotype). **D–E**, *M. synotheoides*; **D**, (H-NYL 19101 – lectotype); **E**, (*Coppins* 3257, E). Scale = 10 μm.

Fig. 31 **D–E** *on following page*

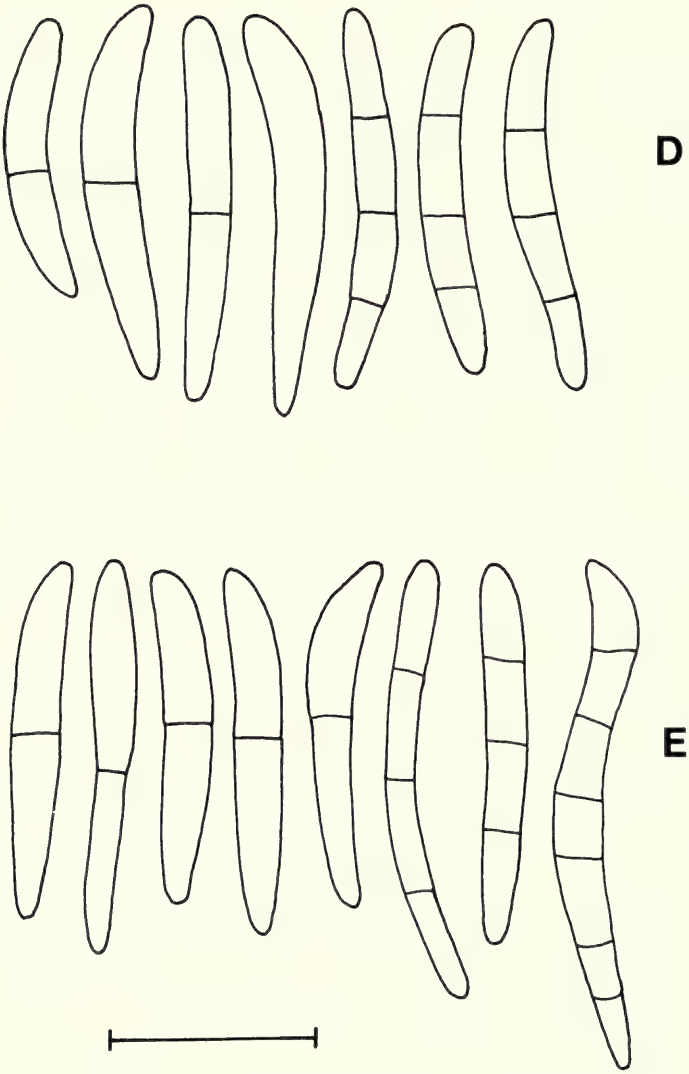


Fig. 31 – *cont.*

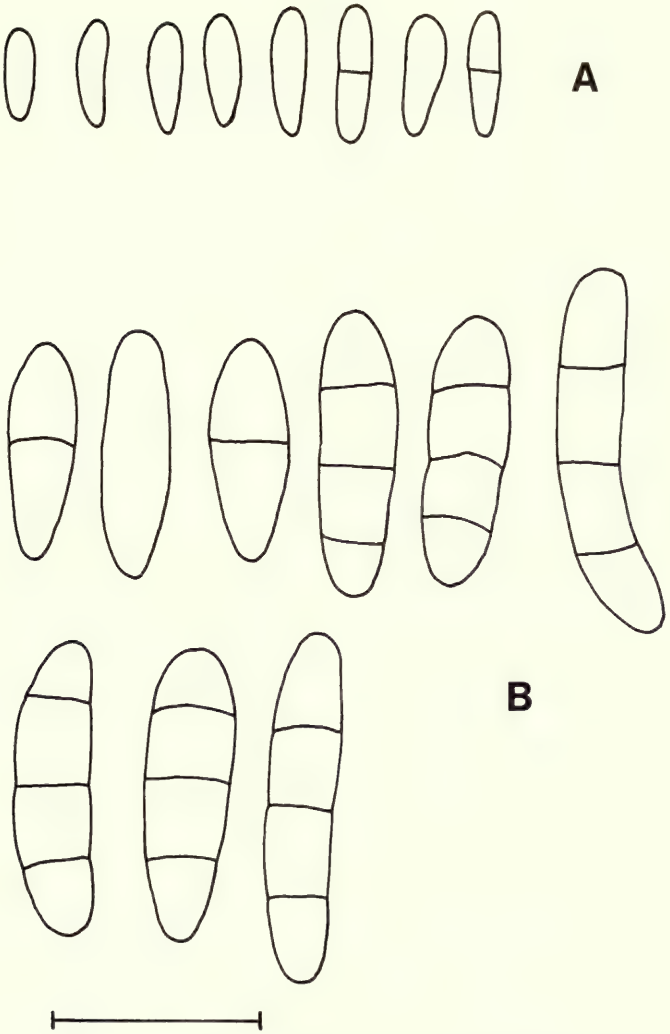


Fig. 32 **A**, *M. tuberculata* (O – lectotype). **B**, *M. ternaria* (*Thomson* 9188, DUKE). Scale = 10 μm.

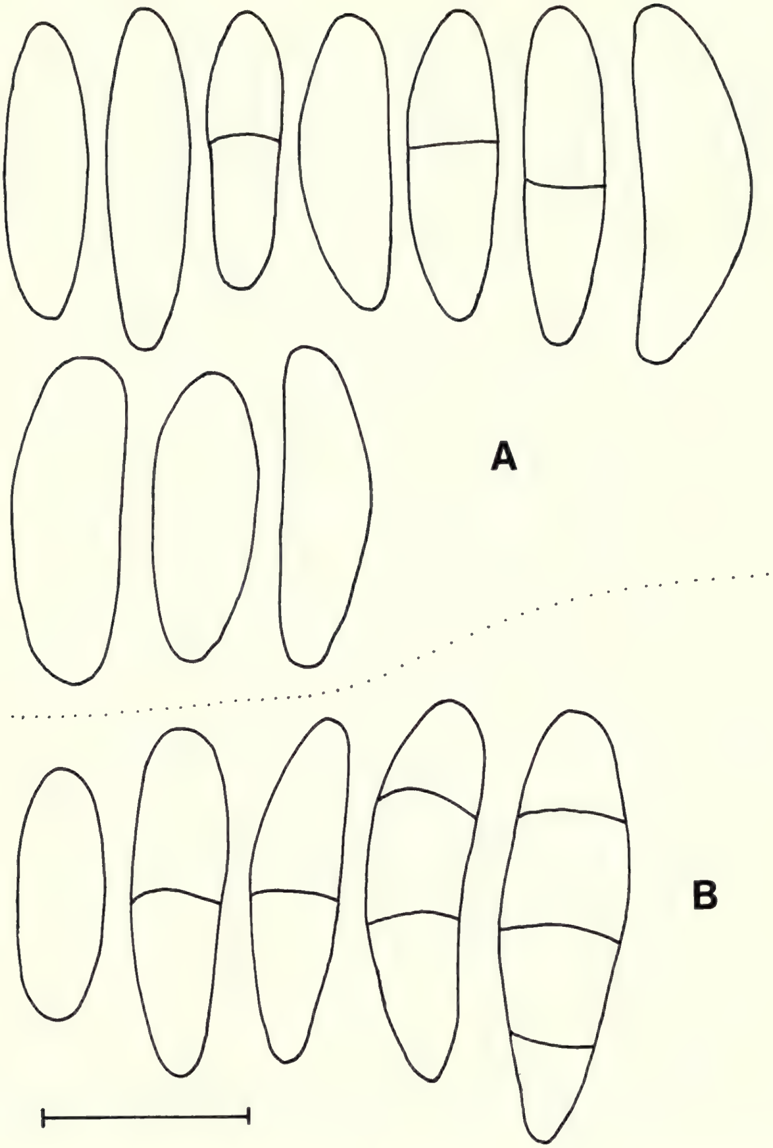


Fig. 33 *M. turfosa*. **A**, (VER – holotype). **B**, (Vězda Lich. Sel. 1135, BM). Scale = 10 μm.

Paraphyses

The paraphyses in *Micarea* are characteristically thin and branched. When measured (in 10% KOH, or ammoniacal erythrosin) at the mid-hymenium they may be very thin and only about 0·6–1 μm wide (e.g. *M. anterior, M. botryoides, M. contexta, M. eximia, M. lithinella, M. misella,* and *M. prasina*), or thin and *c.* 1–1·5 μm wide (e.g. *M. adnata, M. cinerea, M. denigrata, M. intrusa, M. muhrii*, and *M. peliocarpa*), or relatively stout and about 1·5–1·8 μm wide (e.g. *M. assimilata, M. incrassata, M. lignaria, M. osloensis,* and *M. subnigrata*); these measurements relate to paraphyses not coated in pigment. In old, much expanded, apothecia the paraphyses sometimes appear 'stretched' and thinner than normal (especially in the lower half of the hymenium); this phenomenon has frequently been observed in collections of *M. bauschiana, M. sylvicola,* and *M. lignaria*. In many species the paraphyses gradually widen towards their apices, but the apices are never regularly clavate or capitate. This widening is often enhanced by the deposition of closely adhering pigment which sometimes gives the appearance of a 'hood' (e.g. *M. melaena*); such coatings or hoods can be detached by gently boiling and then tapping sections or squash preparations in 50% KOH. In a few cases (e.g. *M. melanobola*) the pigment cannot be separated in this way and appears to be located within the walls of the paraphyses. Paraphyses with dark pigmented apical 'caps', like those found in *Catillaria s. str.* (Killias, 1980: 253), *Buellia*, and many species of *Lecanora*, are not known in *Micarea*.

In all species of *Micarea* a large proportion of the paraphyses are branched, even if the branching is mainly confined to the epithecium. Species with sparingly branched paraphyses include *M. assimilata, M. incrassata* and *M. lignaria*. Anastomozing paraphyses have been observed in all the species, but often the anastomoses are ± confined to the lower third of the hymenium. The degree of branching and anastomosing is difficult to quantify for the practical purposes of identification, but this character can be useful when comparing collections microscopically.

A similarly difficult character is the relative abundance of the paraphyses. The two extremes can be referred to as: (a) 'numerous' – large in number and immediately discernible when observing a mount in 10% KOH at ×400; (b) 'scanty' – few in number and not immediately obvious when observed in the same way. In hymenia with scanty paraphyses the 'extra space' is taken up by hymenial gel or a higher proportion of asci, or a combination of both. The situation in most species lies somewhere between the two extremes. Furthermore, the relative proportions of hymenial gel and asci to paraphyses sometimes increases as the apothecium expands (cf. the above example of *M. bauschiana, M. sylvicola*, and *M. lignaria*). An accurate assessment of the abundance of paraphyses is not usually essential for the routine identification of *Micarea* species, although it can be helpful when comparing difficult, convergent forms of *M. denigrata* and *M. misella* (see couplet 11 of the main key).

In addition to the 'normal' paraphyses described above, the hymenium of several species (e.g. *M. bauschiana, M. botryoides, M. eximia, M. nigella, M. sylvicola*, and *M. tuberculata*) contain scattered individuals, or small fascicles, of rather stout paraphyses. These 'paraphyses' are about 2–3 μm wide and usually more distinctly septate than normal paraphyses. Furthermore (especially in species with a dark hypothecium), they are often coated in pigment throughout their length (Fig. 34), with the result that the hymenium is seen to be intersected by dark vertical streaks. They are mainly found in species with 'scanty' paraphyses, and appear to extend deep into the hypothecium. The elucidation of their true status and function awaits detailed ontogenetic studies, but it is possible that they have a strengthening, spacing or protective function during the maturation of the hymenium from the primary corpus.

Hypothecium

The area of tissue lying below the hymenium, or between the hymenium and the excipulum (if present), is generally referred to by lichenologists as the 'hypothecium'. In many groups of lichenized discomycetes (including the *Lecideaceae*) this area can be divided into an upper, usually narrow, layer containing mainly ascogenous hyphae, and a lower, often much deeper layer of structural tissue (hyphae gelatinised to various extents, according to genus or species). These two layers are often of different colour or colour intensity. Where the two layers are

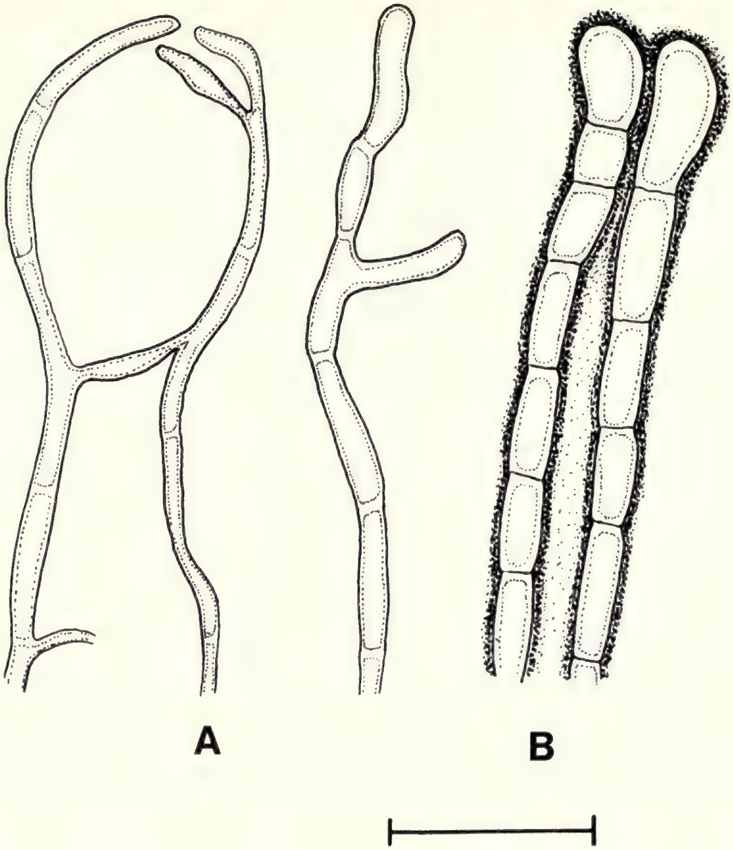


Fig. 34 Two types of paraphyses in *Micarea tuberculata*. **A**, normal, non-pigmented paraphyses. **B**, stout, pigmented paraphyses. Scale = 10 μm.

distinct they have been referred to as the 'subhymenium' and 'hypothecium' respectively (e.g. Hertel, 1977*b*). The term 'hypothecium' in this context has been substituted by many students of non-lichenised discomycetes by the term 'medullary excipulum' (Korf, 1973), and was called the 'ental excipulum' by Eckblad (1968). In *Micarea* the two layers are well-differentiated in only a few species (e.g. *M. crassipes*); and in the present work 'hypothecium' refers to all ascocarp tissue lying below the hymenium, apart from the excipulum (where present). This same terminology was adopted in the recent study of *Catillaria* by Kilias (1981).

The hypothecium in *Micarea* is composed of deeply staining (e.g. in LCB and ammoniacal erythrosin), swollen-celled ascogenous hyphae (*c.* 2–5 μm wide) and moderately staining, slender 'structural' hyphae (*c.* 0·7–2 μm wide; slightly varying in width according to species), embedded in a gelatinous matrix. In species with a colourless or pale hypothecium the matrix is ± dispersed in K and the hyphae are then clearly visible (×400). In some species with a coloured hypothecium the pigment may be ± evenly distributed through the matrix and the hyphae are similarly distinct in K (e.g. *M. eximia, M. olivacea*, and *M. turfosa*). However, in the majority of species with a darkly coloured hypothecium (e.g. *M. assimilata, M. botryoides, M. melaena, M. myriocarpa*, *M. nigella*, *M. sylvicola*, and *M. tuberculata*) the pigment, although present in the matrix, exists as a strongly adhering coat around the hyphae, such that the hyphae appear thick-walled and broad (*c.* 1·5–4 μm). The pigment coatings tend to bind the hyphae together so that they are often indistinct in K. For the routine identification of *Micarea* species it is not essential to know the location of pigment (i.e. ± evenly distributed through the gel-matrix *versus* tightly bound to hyphae) but such knowledge is sometimes of supplementary value, e.g. when comparing *M. eximia* versus *M. nigella* and *M. olivacea* versus *M. tuberculata*.

A more important diagnostic character in *Micarea* is the colour of the hypothecium in water mounts, and the corresponding colour changes obtained by the addition of KOH and HNO_3. A discussion of the pigments involved is given under 'chemistry'.

The height of the hypothecium (in vertical section) is largely dependent on the overall size and (especially in species with a poorly developed excipulum) convexity of the apothecium. The measurements given in the species descriptions relate to normally developed, non-tuberculate apothecia. This character is often very variable for a given species and consequently of little diagnostic value when comparing closely similar species. One exception to this is the case of *M. contexta* (20–90 μm) versus *M. melaena* (80–160 μm).

In Lugol's iodine the hypothecial tissues are non-amyloid, although there is sometimes a faint bluing in the vicinity of ascogeneous hyphae (especially in the upper part of the hypothecium).

Excipulum

The size and distinctiveness of the excipulum ('ectal excipulum') in *Micarea* varies greatly according to species and the age of the apothecium. In species such as *M. cinerea, M. crassipes* (Fig. 4B), *M. peliocarpa*, and *M. ternaria* the excipulum is sufficiently well developed that their young apothecia are often weakly or distinctly (*M. crassipes*) marginate in outward appearance. However, even when well developed and initially distinct, the excipulum may become reflexed and ± occluded as the apothecium expands and increases in convexity (Fig. 3A–B) or becomes tuberculate (Fig. 3C). In many species the excipulum is always extremely reduced or absent (Fig. 4A).

When present, the excipulum is composed of outwardly radiating branched and anastomosing hyphae that ± separate in K. The hyphae closely resemble paraphyses, but are usually more dense and more richly branched. With markedly convex apothecia it can be difficult to distinguish between reflexed portions of the hymenium and what might be an excipulum. In such cases the excipulum (if present) can be identified in good thin sections by the absence of asci and a negative (non-amyloid) reaction to Lugol's iodine. The excipulum often differs in colour or colour intensity from the hymenium, although a similar colour difference may sometimes be shown by reflexed parts of the hymenium.

In *M. crassipes* and rare forms of *M. lignaria* ('f. *gomphillacea*') the excipular and hypothecial tissues become vertically extended to form a stipe (Figs 3E, 4B).

Anamorphs (conidial states)

With a few noteworthy exceptions, such as Lindsay (1859, 1872) and Glück (1899), the conidial states (anamorphs) of lichenized fungi have received little detailed attention from taxonomists. Several recent monographic studies have shown that anamorphs can provide useful characters at various hierarchial levels of classification and the reader is referred to Vobis (1980) and Vobis & Hawksworth (1981) for further background information on the conidial states of lichens.

Within the genus *Micarea* there is a diverse array of anamorphic forms, possibly unrivalled by any other genus of lichens, except perhaps for some of the genera in the Asterothyriaceae (Vězda, 1979). Information gained from the study of anamorphs has proved invaluable to me for the delimitation of species in *Micarea*; indeed, several species frequently occur without apothecia but with numerous pycnidia, such that a detailed knowledge of the latter is often essential for their identification (see 'key to species without apothecia').

Conidiomata

The conidiomata are usually pycnidial, and are globose, ovoid, doliiform, or ceriberiform in shape. They may be immersed (or partly so) within the thallus or substratum, sessile, or borne on stalks (pycnidiophores). When stalked, the pycnidia are usually ± doliiform and the stalk-tissue is comprised of loosely interwoven hyphae bound by a gel matrix which is often pigmented. In addition, the 'stalk-part' often includes effete pycnidia (Fig. 35B–D). The stalks are sometimes branched due to the simultaneous development of two (or more) pycnidia at the

Table 1 Conidial states (anamorphs) found in European species of *Micarea*.

		Conidium – type		
Micarea	micro-	meso-	macro-	Stalked pycnidia
adnata		+	+	
alabastrites	+		+	
anterior	+	+		+
assimilata	+			
bauschiana	+	?+		
botryoides		+		+
cinerea	+		+	
contexta	+	+		
crassipes		+		
curvata				
denigrata	+	+	+	
elachista	+	+		
eximia		+		
globulosella	+	+		
hedlundii		+		+
incrassata	+			
intrusa				
leprosula				
lignaria	+	+	+	
var. *endoleuca*	+			
lithinella	+			
lutulata		+		
melaena	+		+	
melaenida	+			
melaeniza		+		+
melanobola	+	+		
misella	+	+		+
muhrii	+			
myriocarpa		+		±
nigella		+		+
nitschkeana	+	+	+	
olivacea		+		
osloensis				
peliocarpa	+		+	
prasina	+	+		
pycnidiophora		+		+
rhabdogena	+	+		
stipitata		+		+
subleprosula				
subnigrata	+		+	
subviolascens				
sylvicola		+		
synotheoides	+	+		
ternaria		+		
tuberculata		+		
turfosa	+			
Total (species)	25	28	9	9

apex of stalk tissue (Fig. 35F) or at the apex of an old pycnidium (Fig. 35D). Stalked pycnidia are apparently rare in other genera of crustose lichens (or related fungi). However, I have seen branched pycnidiophores associated with lignicolous *Chaenothecopsis* spp. growing on the moribund thalli and ascocarps of *Chaenotheca* spp. (several collections in E).

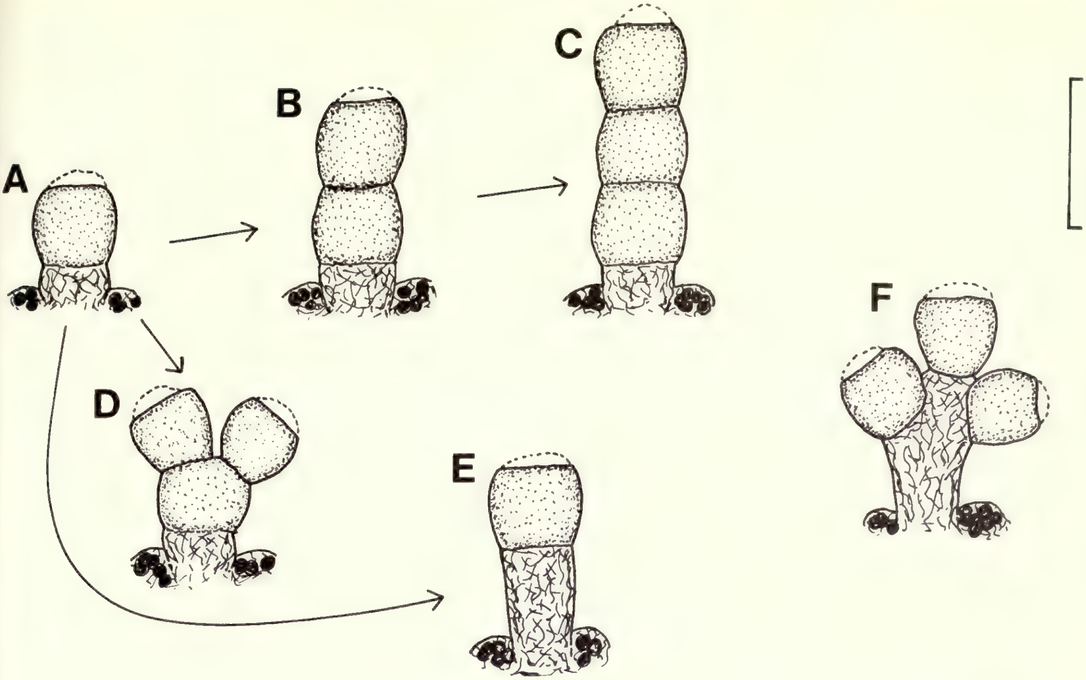


Fig. 35 *Micarea botryoides*, conidiomata: diagram showing the various means of 'stalk' formation and branching (see text for further details). Scale = 100 μm.

The pycnidia of species which consistently lack pigment in their apothecia (e.g. *M. adnata, M. alabastrites, M. pycnidiophora*, and *M. stipitata*) correspondingly lack pigment in their wall tissues. In species with coloured apothecia the pycnidial walls are usually (at least in part) coloured also. For a given species the pigment involved is usually that found in the hymenium (or epithecium) of the apothecia, but in a few cases (e.g. *M. lutulata*) it is the pigment found in the hypothecium which is involved. The link between apothecial and pycnidial pigmentation helps distinguish pycnidia belonging to a *Micarea* from any intermixed pycnidia belonging to a non-lichenized or parasitic fungus. It further helps to distinguish the pycnidia belonging to the different species of *Micarea* in mixed populations; for example, the stalked pycnidia of *M. misella* (walls olivaceous, K+ violet) are often found intermixed with those of other species such as *M. anterior* (walls reddish brown, K−) and *M. melaeniza* (walls dark olivaceous, K−).

When a pycnidium is deeply immersed in the thallus it is often only the uppermost part around the ostiole which is coloured, and likewise, if the pycnidium is semi-immersed it is often only the upper, exposed part which is coloured. With the exception of the species that are characteristically devoid of pigment and some forms of other species in deep shade, the walls of sessile or stalked pycnidia are coloured more or less throughout.

As mentioned above, the conidiomata of *Micarea* species are pycnidial, but there is one exception to this. *M. adnata* has two anamorphic states: one in which the conidia (mesoconidia) are produced internally in immersed pycnidia; and another where the conidia (macroconidia) are borne externally on cushion-like sporodochia which resemble small apothecia. This latter state could be considered to be a hyphomycetous anamorph but comparative ontogenetic studies are required to investigate the theoretical possibility that these sporodochia have evolved from pycnidial conidiomata by an exertion of the 'hymenium', and a thickening of the subtending wall-tissue to form a supporting cushion (Fig. 36). Unfortunately this hypothesis is not supported by intermediate forms in other species, although the pycnidia (with filiform or curved-hamate macroconidia) of, for example, *M. cinerea* and *M. peliocarpa* often have widely

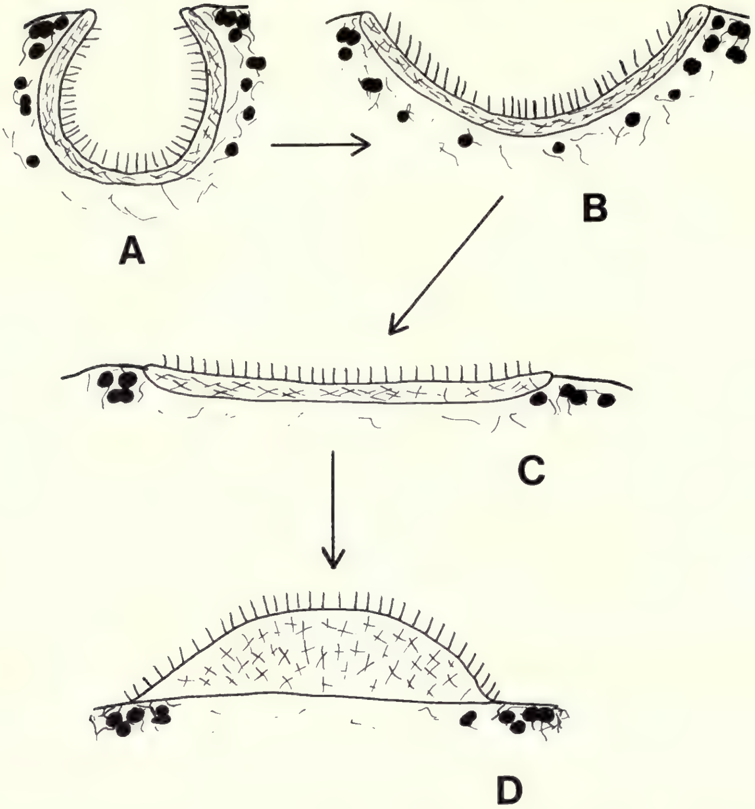


Fig. 36 Suggested pathway for evolution of a sporodochium (**D**, as in *M. adnata*) from a pycnidium (**A**). The step **A→B** can be seen in the macroconidial conidiomata of e.g. *M. cinerea* and *M. peliocarpa,* and the mesoconidial conidiomata of e.g. *M. denigrata* and *M. sylvicola*. No structure equivalent to '**C**' is known from *Micarea.*

gaping ostioles which eventually expose the 'hymenium'. The often dubious distinctions between pycnidia, acervuli, and other types of conidiomata are discussed by Nag Raj (1981). Although the sporodochial anamorph of *M. adnata* has unusually large, oblong-ellipsoid conidia and the longest conidiogenous cells known in the genus, there seems to be no fundamental difference in these features from those in other *Micarea* anamorphs, and the mode of conidiogenesis is apparently the same in all cases (see below).

Conidia

Vobis & Hawksworth (1981) estimate that perhaps as many as 8000 species of lichenized fungi have conidial anamorphs, and that in most cases a given species has only one conidium type. However, it is becoming increasingly evident that a large number of lichens (especially crustose lichens) have two conidium types, although many of the examples have not yet been notified in the literature. Some examples from my own studies include *Anisomeridium biforme, A. juistense, Catillaria globulosa, Lecania cyrtellina, Lecanora quercicola,* and *Opegrapha niveoatra*. Hedlund (1895) found *M. denigrata* and *M. prasina* to each have two conidium types and during the present study 16 of the 45 European species of *Micarea* have been found to have two conidium types. Even more surprising has been the discovery that three species (*M. denigrata, M. nitschkeana*, and *M. lignaria*) each have three conidium types (Figs 42, 45), and to my knowledge these are the first reported instances of fungi (whether lichenized or not) with more than two pycnidial (coelomycetous) anamorphs. There are, however, a few species of sooty mould (e.g. in the *Metacapnodiaceae*) which have three hyphomycetous anamorphs (Hughes 1972, 1976).

The main distinguishing features of the three conidium types found in *Micarea* are as follows (see Figs 37–52 for example): *Microconidia*, narrowly cylindrical or narrowly fusiform, aseptate, eguttulate and not constricted in the middle, mostly in the range 3–8×0·5–1 μm; produced in small immersed or ± sessile pycnidia, mostly *c.* 20–60 μm diam. *Mesoconidia,* variable in shape, e.g. cylindrical, oblong, ovoid-oblong or obovoid-oblong, aseptate, often biguttulate and (or) slightly constricted in the middle; produced in small to large, immersed, sessile or stalked pycnidia. All conidia found in stalked pycnidia are included here. *Macroconidia,* mostly filiform or curved and often septate, or helicoid and septate (*M. subnigrata* (p. 183)); produced in medium-sized to large (often up to 200 μm diam or more) pycnidia. Also included here are the large, aseptate, eguttulate, oblong-ellipsoid conidia produced by the sporodochia of *M. adnata*.

In all cases no single pycnidium has been found to contain more than one conidium type. A few specimens of *M. denigrata* and *M. nitschkeana* have been found with all three anamorphs on the same thallus; but such occurrences are rare and it is more usual to find just one or two of them. A few species (e.g. *M. assimilata, M. crassipes*, and *M. incrassata* appear to have only one anamorphic state, with conidia somewhat intermediate between microconidia and mesoconidia as defined above; thus the assignment of their conidia to one or other of these types (Table 1) must be considered tentative. The distinction between the three conidium types (especially micro- and mesoconidia) is most obvious when two or three of them occur on the same thallus. The use of the terms 'micro-', 'meso-' and 'macroconidia' are here applied solely to the conidium types found in *Micarea* – they may not necessarily be analogous to their use in other lichenized or non-lichenized fungi. Table 1 indicates the conidium type(s) known for each of the European species of *Micarea*, and from this a numerical summary of the various known combinations is as follows:

Combination of conidium types (anamorphs)	Number of species (holomorphs)
Micro- + meso- + macro-	3
Micro- + meso-	10
Micro- + macro-	5
Meso- + macro-	1
Micro- only	6
Meso- only	14
Macro- only	0
Anamorph(s) unknown	6

The role of each of the conidium types is as yet unknown. Vobis (1977) obtained successful germination and subsequent growth of mycelium from the macroconidia of *Lecanactis abietina*, but was unable to germinate the microconidia of the same species. His results suggest that the former may well act as asexual propagules, and the latter as spermatia in sexual reproduction. It seems most likely to me that the microconidia of *Micarea* species are spermatia. As to whether or not they are essential components of the sexual reproductive process is much less certain; 21 of the treated species are not known to produce microconidia.

The role of conidia as asexual propagules is still a matter of much debate and speculation among lichenologists, but such a role (at least in certain cases) can be inferred from the fact that a few crustose species (e.g. *Lecanactis subabietina* and an undescribed *Bacidia*) are not known to have apothecia or vegetative diaspores (i.e. soredia, isidia, etc.) but always have numerous pycnidia. To such examples can be added the numerous crustose lichens whose apothecia are known, but which commonly occur as sterile populations with numerous pycnidia, e.g. *Anisomeridium juistense* (macroconidial state), *Arthonia phaeobaea, A. spadicea, Bacidia arnoldiana, B. carneoglauca, B. trachona, Cliostomum graniforme, C. griffithii, Lecanactis abietina, Lecidea erratica, Opegrapha niveoatra, O. vermicellifera,* and *O. vulgata*. This last group also includes *Micarea botryoides, M. denigrata, M. misella, M. pycnidiophora*, and *M. stipitata*, all of which commonly occur with abundant mesoconidia-containing pycnidia and few (if any) mature apothecia.

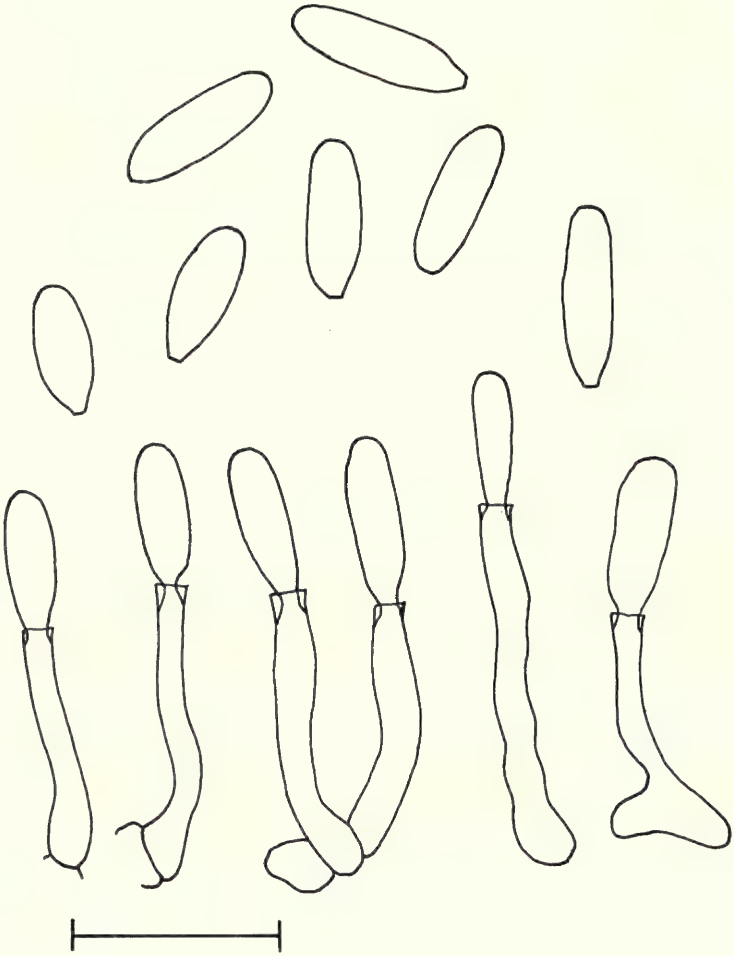


Fig. 37 *M. adnata* (E – holotype), macroconidia and conidiogenous cells. Scale = 10 μm.

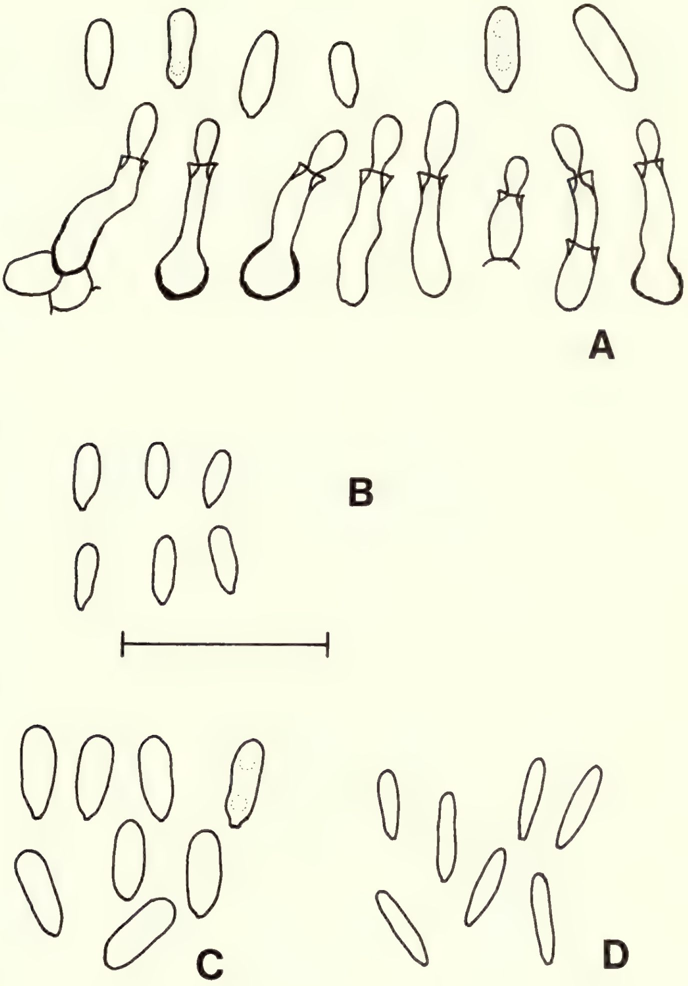


Fig. 38 **A**, *M. botryoides* (*Coppins* 8429, E), mesoconidia and conidiogenous cells. **B**, *M. melaeniza* (S – holotype), mesoconidia. **C–D**, *M. anterior* Sweden, Ångermanland, Långsele, 1892, *Hedlund,* S); **C**, mesoconidia; **D**, microconidia. Scale = 10 μm.

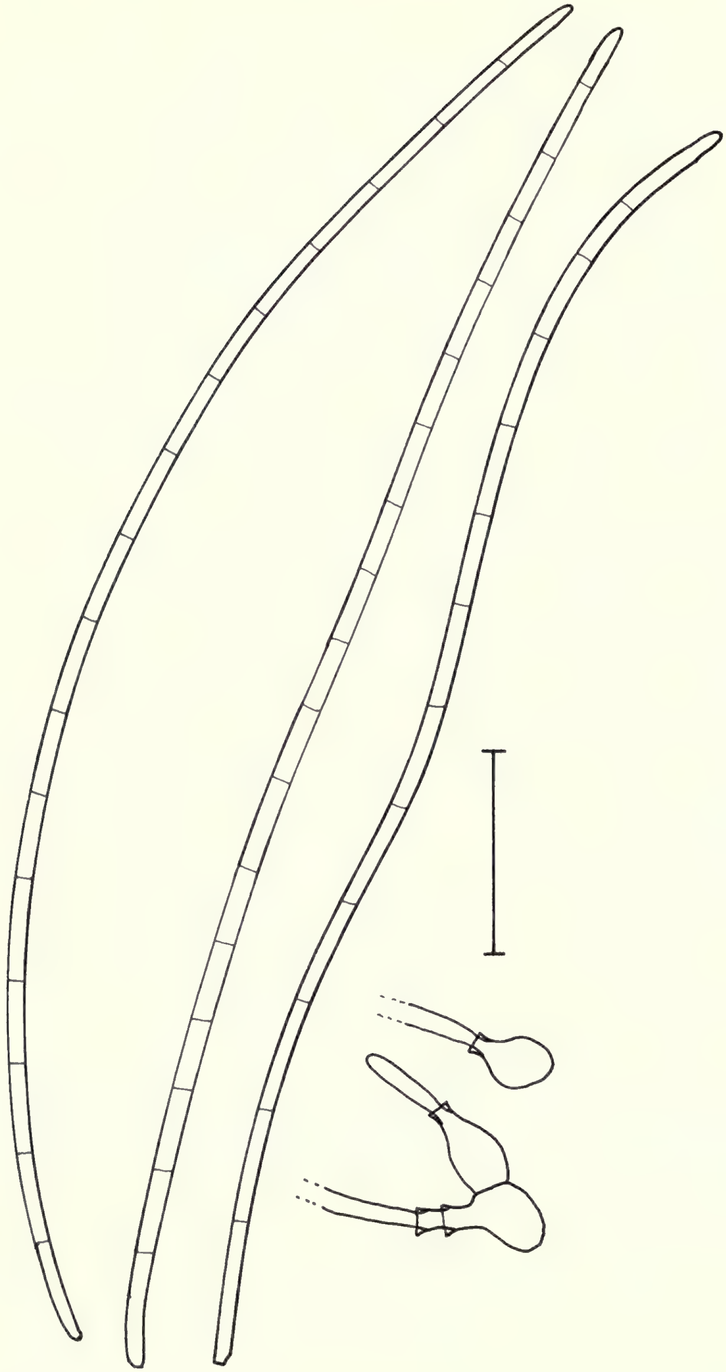


Fig. 39 *M. cinerea* (*Coppins* 2533, E), macroconidia and conidiogenous cells. Scale = 10 μm.

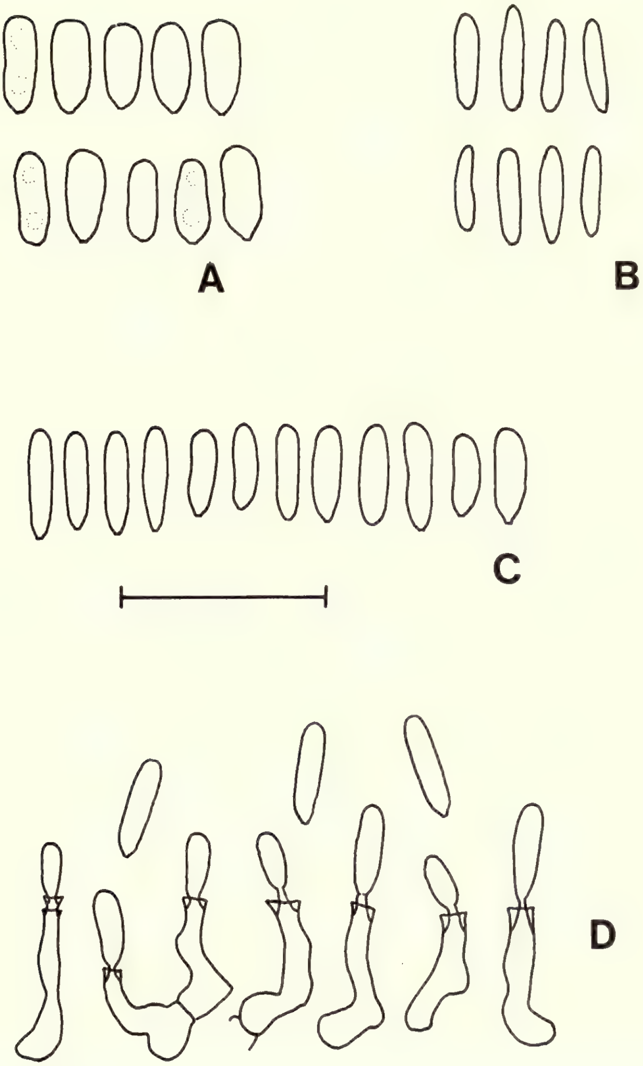


Fig. 40 **A–B**, *M. contexta* (S – lectotype); **A**, mesoconidia; **B**, microconidia. **C**, *M. eximia* (Malme Lich. suec. exs. 26, C), mesoconidia. **D**, *M. bauschiana* (*Coppins* 4111, E), microconidia and conidiogenous cells. Scale = 10 μm.

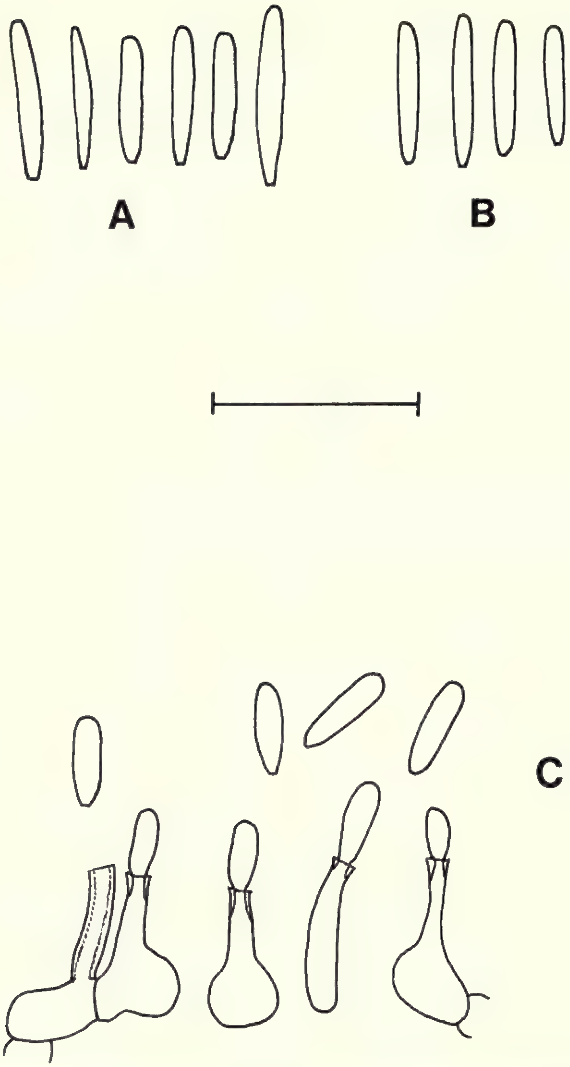


Fig. 41 **A–B**, *M. incrassata*, microconidia; **A**, (S – holotype); **B**, (Kerguelen, 1875, *Eaton,* E). **C**, *M. crassipes* (Vězda Lich. Sel. 11, BM), (?)mesoconidia and conidiogenous cells. Scale = 10 μm.

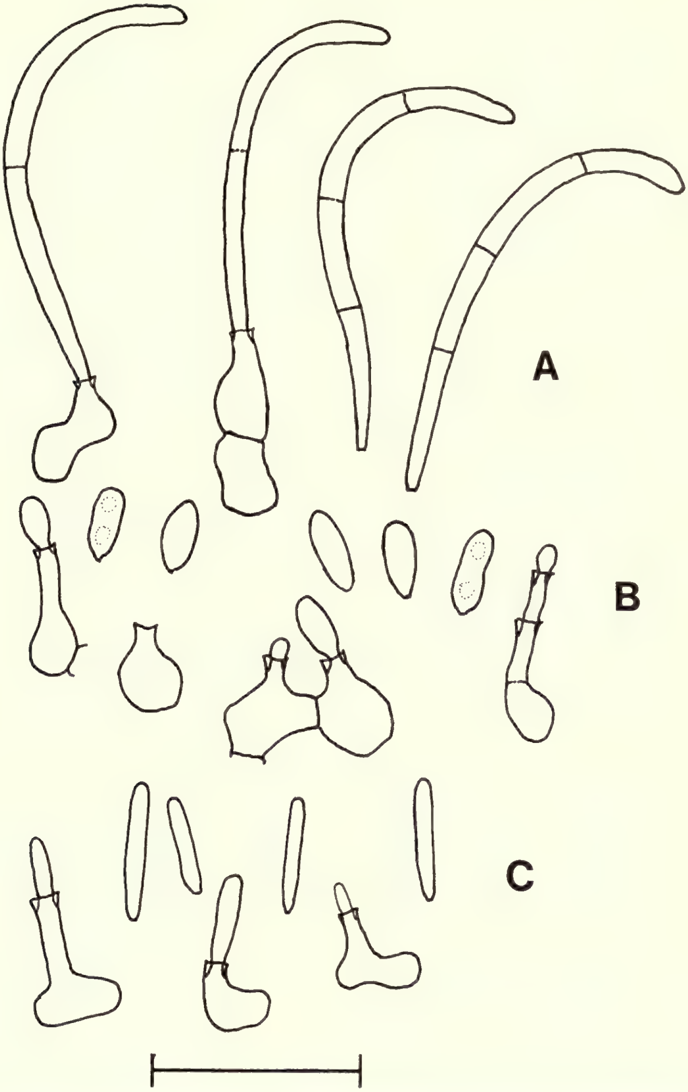


Fig. 42 *M. denigrata* (*Coppins* 1888, E), conidia with conidiogenous cells; **A**, macroconidia; **B**, mesoconidia; **C**, microconidia. Scale = 10 μm.

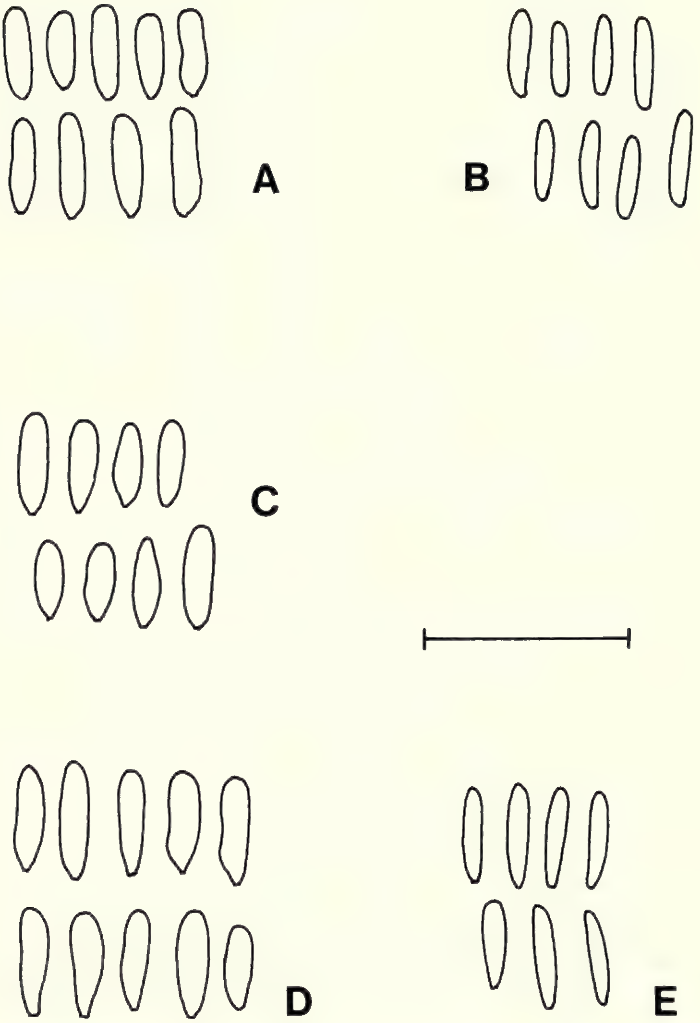


Fig. 43 **A–B**, *M. globulosella* (Czechoslovakia, Slovakia, Vysoké Tatry, 1879, *Lojka*, BM); **A**, mesoconidia; **B**, microconidia. **C**, *M. globulosella* (S – lectotype), mesoconidia. **D–E**, *M. synotheoides* (*Coppins* 2942, E); **D**, mesoconidia; **E**, microconidia. Scale = 10 μm.

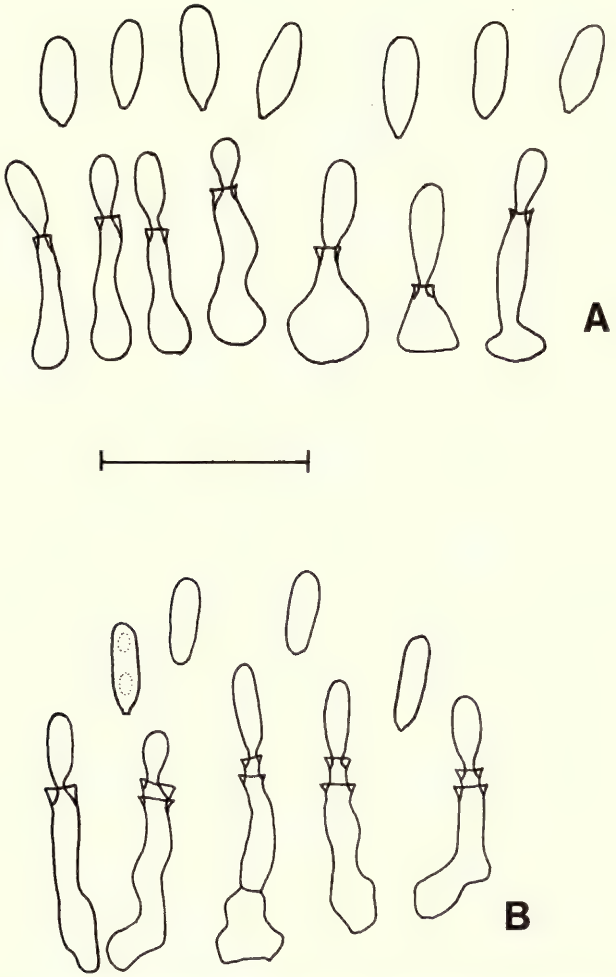


Fig. 44 **A**, *M. hedlundii* (UPS – holotype), mesoconidia and conidiogenous cells. **B**, *M. lutulata* (Wales, Pembroke, Tycanol, 1980, *James*, BM), mesoconidia and conidiogenous cells. Scale = 10 μm.

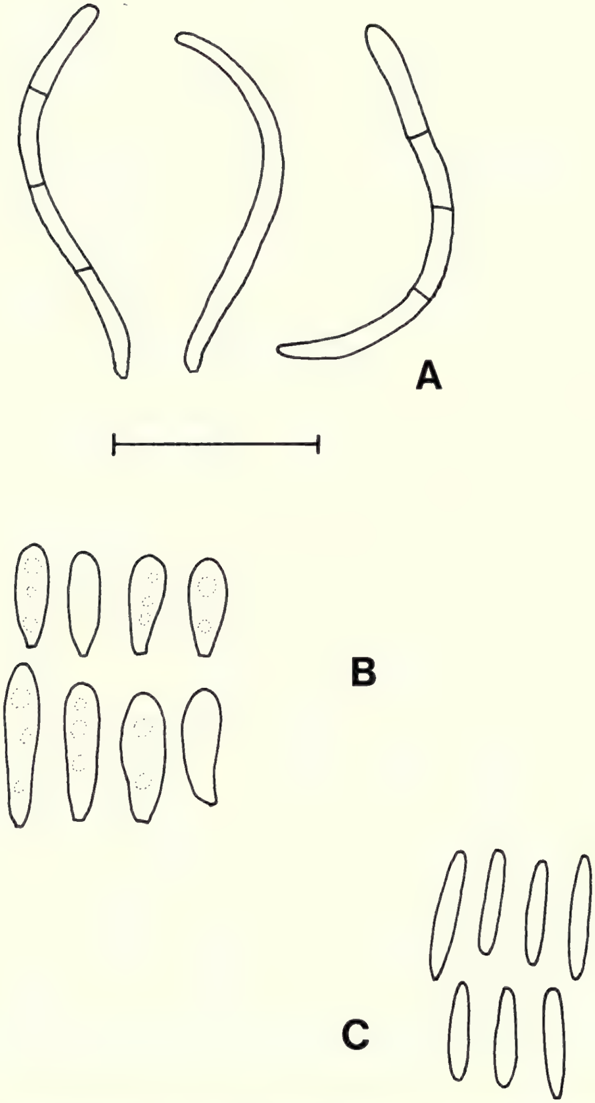


Fig. 45 *M. lignaria.* **A**, macroconidia (*Coppins* 4658, E). **B**, mesoconidia (*Coppins* 8436, E). **C**, microconidia (*Coppins* 8952, E). Scale = 10 μm.

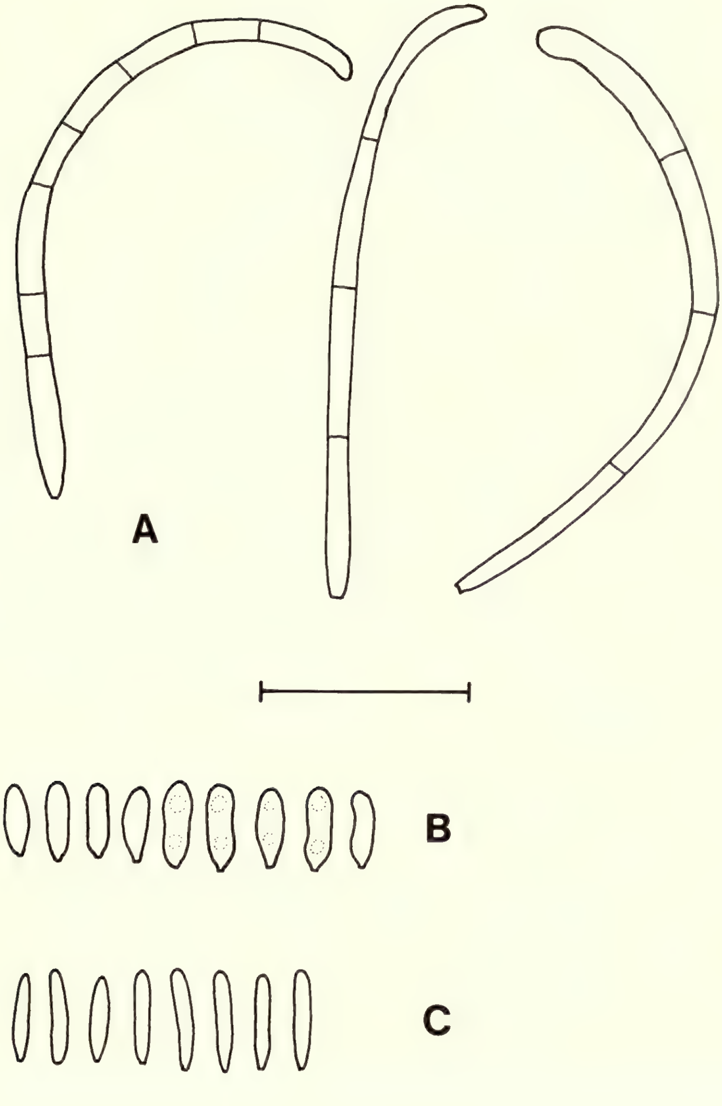


Fig. 46 **A**, *M. melaena* (*Coppins* 6041, E), macroconidia. **B–C**, *M. melanobola* (H-NYL 2164 – lectotype); **B**, mesoconidia; **C**, microconidia. Scale = 10 μm.

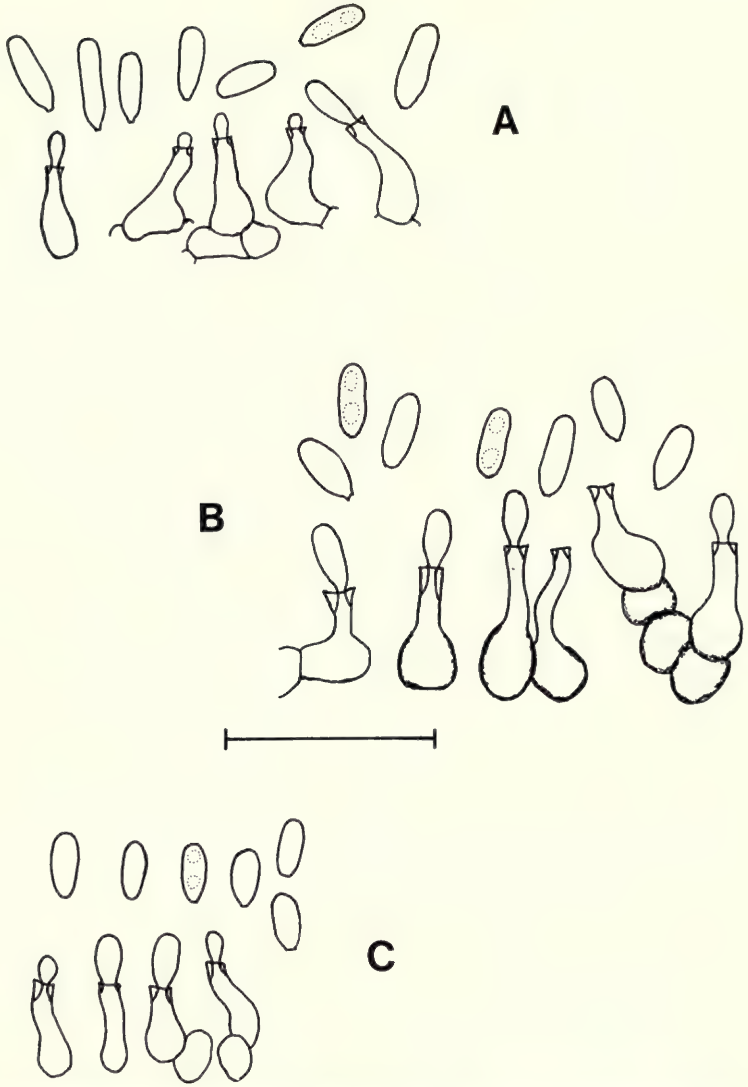


Fig. 47 **A**, *M. olivacea* (BM – holotype), mesoconidia and conidiogenous cells. **B**, *M. nigella* (E – holotype), mesoconidia and conidiogenous cells. **C**, *M. myriocarpa* (*Coppins* 8939, E), mesoconidia and conidiogenous cells. Scale = 10 μm.

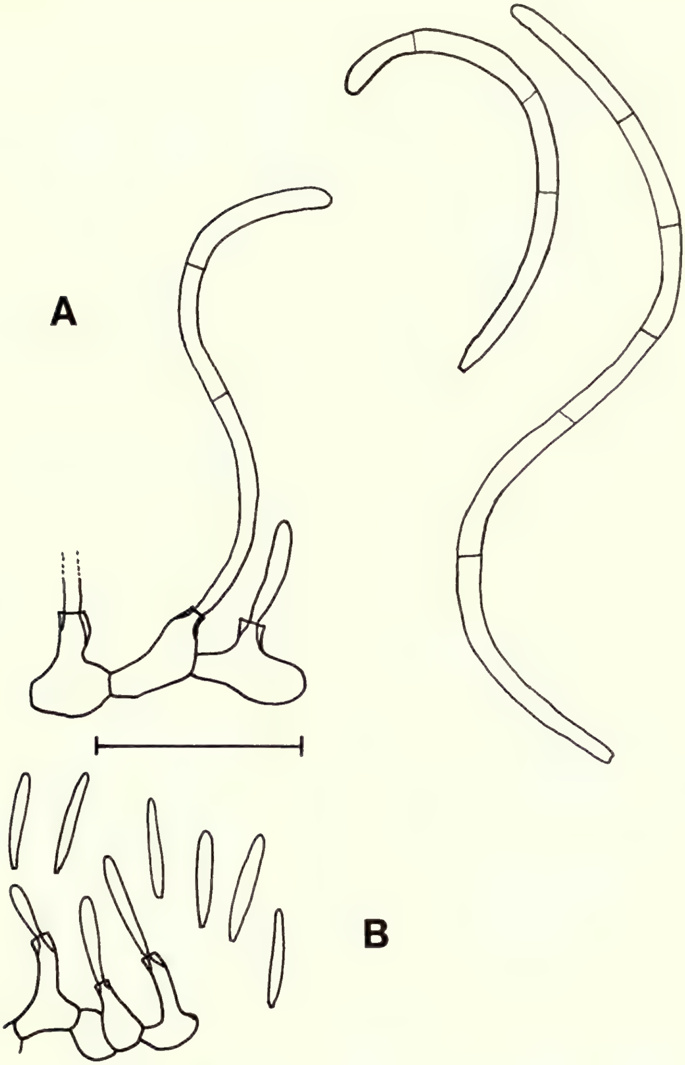


Fig. 48 *M. peliocarpa* (England, New Forest, Great Wood, Bramble Hill Walk. 1970, *Coppins et al.*, E). **A**, macroconidia and conidiogenous cells. **B**, microconidia and conidiogenous cells. Scale = 10 μm.

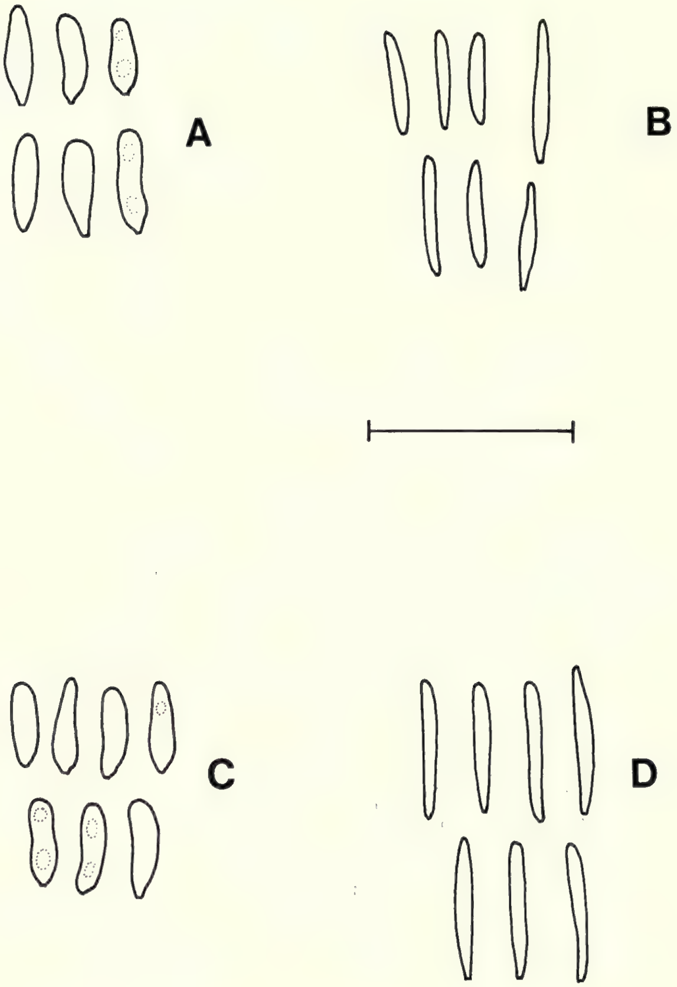


Fig. 49 **A–B**, *M. prasina* (GZU – holotype of *M. polytrichi*); **A**, mesoconidia; **B**, microconidia. **C**, *M. prasina* (*Coppins* 8009, E), mesoconidia. **D**, *M. prasina* (*Coppins* 2835, E), microconidia. Scale = 10 μm.

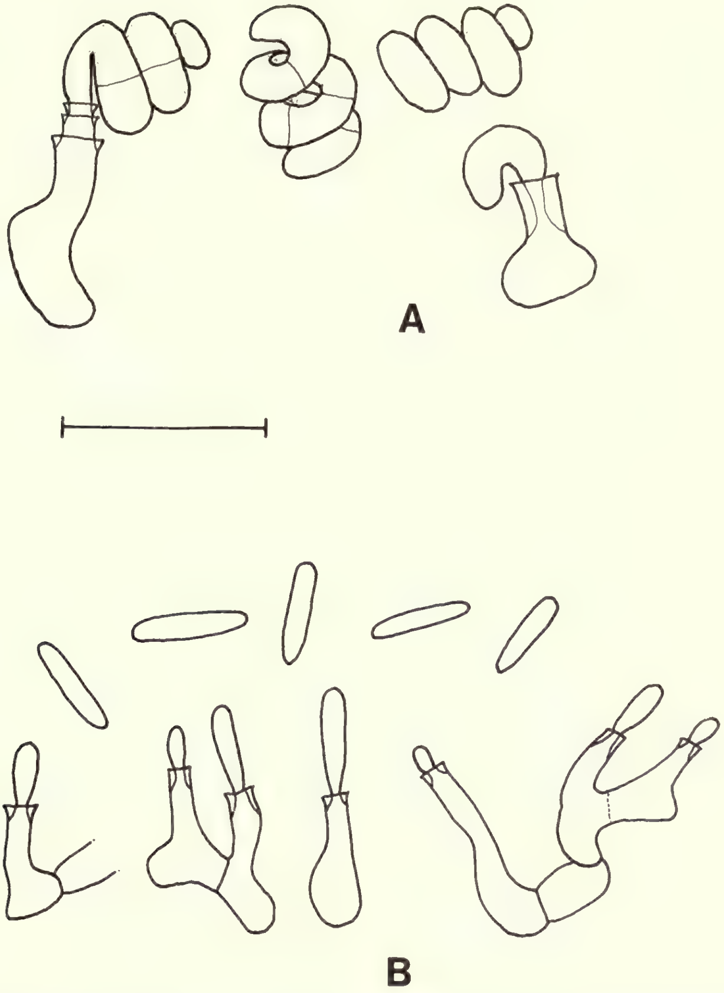


Fig. 50 *M. subnigrata* (*Coppins 8417, E*). **A**, macroconidia and conidiogenous cells. **B**, microconidia and conidiogenous cells. Scale = 10 μm.

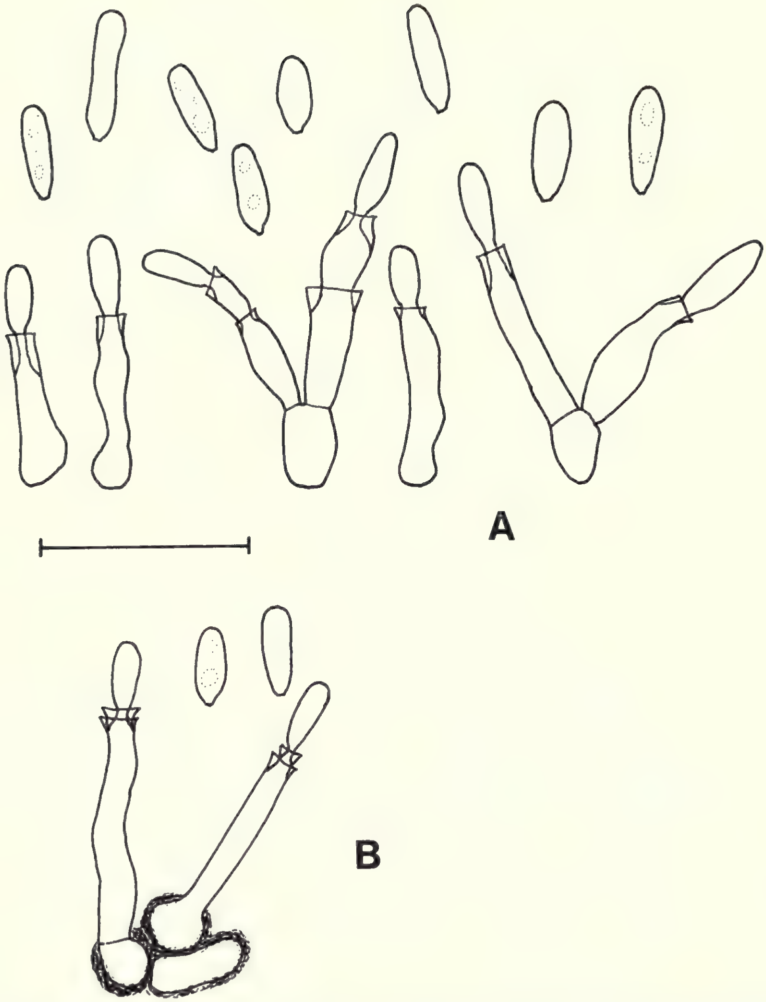


Fig. 51 **A**, *M. sylvicola* (*Muhr* 2579, E), mesoconidia and conidiogenous cells. **B**, *M. tuberculata* (O – lectotype), mesoconidia and conidiogenous cells. Scale = 10 μm.

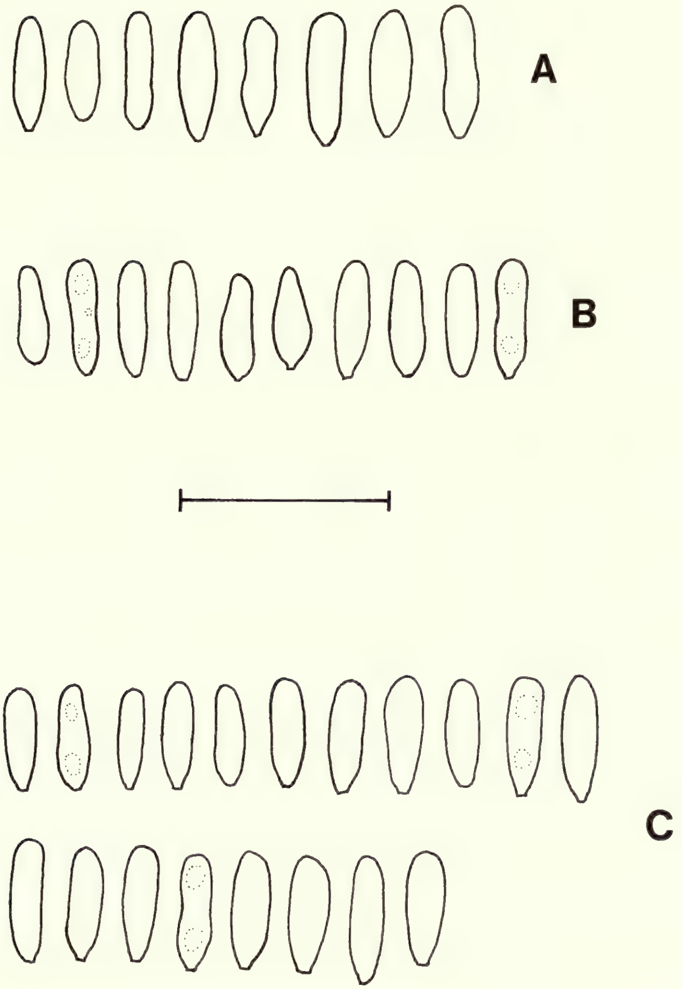


Fig. 52 **A–B**, *M. ternaria*, mesoconidia; **A**, (H-NYL 18682 – holotype); **B**, (*Thomson* 9188, DUKE). **C**, *M.* aff. *ternaria* (Fair Isle, 1976, *Duncan*, BM), mesoconidia. Scale = 10 μm.

In the case of *M. denigrata* it is a general rule (but with exceptions) that when on worked wood (fence-posts, garden furniture, window frames, etc.) its thallus has numerous pycnidia (with mesoconidia) and often few (if any) mature apothecia. On natural substrata (e.g. fallen tree trunks in old woodlands) pycnidia with microconidia or macroconidia are more prevalent, although they are usually relatively fewer in number and associated with numerous apothecia. It seems highly likely that the success of *M. denigrata* as a primary coloniser of newly available substrata is largely due to the successful role of its mesoconidia as asexual propagules. Its microconidia probably function as spermatia, but the function of the macroconidia is less obvious, although I suspect that they, like the mesoconidia, act as asexual diaspores (perhaps in a different way).

Another observation pertinent to this discussion is that I have frequently observed the meso- and macroconidia of *Micarea* species being extruded through the ostioles of the pycnidia as white mucilaginous blobs; such phenomena are usually seen after periods of wet weather. It is tempting to suggest that these extrusions facilitate dispersal beyond the limits of the parent thallus by the action of rain or passing arthropods and mollusca. Dispersal by invertebrates may be of especial importance for species such as *M. botryoides*, which occur in sheltered situations rarely subjected to rain-wash. I have only rarely observed microconidia being extruded as white blobs, thus suggesting that there is no need for them to be dispersed beyond the limits of the parent thallus. Indeed, if microconidia do function as spermatia, and if the mycobiont of the *Micarea* is homothallic, there would be no requirement for them to be dispersed more than a few millimetres.

Conidiogenous cells

The conidiogenous cells of *Micarea* species are always phialidic, although in many cases the phialides are seen to undergo 'percurrent proliferation' (Figs 42B, 44B). The conidiogenous cells belong to Types I or II of Vobis & Hawksworth (1981) and arise from the inner wall of the pycnidium (or on the outer surface of the sporodochium in *M. adnata*). Their subtending cells are never sufficiently regular in shape for them to be termed 'conidiophores'. In several species whose pycnidial walls are intensely pigmented the bases of the conidiogenous cells are often similarly pigmented (Figs 47B, 51B). The nearest approach to the differentiation of wall-tissue from a conidiogenous layer is found in the thick-walled pycnidia of *M. elachista*.

There is much variety in the shape of conidigenous cells (e.g. ampulliform, doliiform, lageniform, cylindrical) and there is sometimes much variation within a single pycnidium (Figs 42B, 44A). Conidiogenous cells with long cylindrical necks often have swollen bases (Figs 38A, 47B, 51B). Although critical observations and measurements have not been made for all species, the size and shape of conidiogenous cells have rarely been found to be useful characters for the separation of closely similar species. However, one exceptional case is that of saxicolous forms of *M. olivacea* (Fig. 47A) versus *M. tuberculata* (Fig. 51B), in which the conidiogenous cells of the latter are much longer.

Chemistry

The discussions below are presented under two sub-headings. The first deals with 'lichen substances', which are readily extractable in acetone and identifiable by thin-layer chromatography (t.l.c.; see 'Methods'). The second part deals with pigments that cannot be analysed in this way; their chemical nature is at present unknown and they can only be characterised by their colour in water and subsequent reactions with reagents such as K and HNO_3.

Lichen substances

Prior to the present studies there is little evidence in the literature to suggest that species of *Micarea* contain any lichen substances. However, there are a few hints given in some early descriptions: for example, Leighton (1879: 362) gives 'K+ yellow, C+ orange-red' reactions for *Lecidea milliaria [Micarea lignaria]*, which probably relate to his specimens of the var. *endoleuca*. The only reported t.l.c. analysis of a *Micarea* appears to be that of Huneck &

Table 2 Chemical content and corresponding spot test reactions of European species of *Micarea* known to contain lichen substances. +, present; ±, presence variable and sometimes absent; ?, present occasionally as trace amounts or contaminant; R, red; Y, yellow; fY, faint yellow; O, persistent orange; ( ) reactions not obtainable in many collections; *, including 3 or 4 accessory substances.

	alectorialic*	argopsin	gyrophoric	xanthones	prasina unk. A	prasina unk. B	prasina unk. C	Thallus reactions			Apothecia reactions
								K	C/KC	PD	C
alabastrites			+					—	R	—	R
cinerea			+					—	R	—	R
curvata			+					—	R	—	R
denigrata			+					—	R	—	R
globulosella			+					—	R	—	R
hedlundii						?		—	—	—	—
leprosula		+	+					—	R	R	R
lignaria		+						—	—	R	—
var. *endoleuca*				+				fY	O	—	—
melaena			+					—	R	—	—
misella			±					—	(R)	—	(R)
nitschkeana			+					—	R	—	R
peliocarpa			+					—	R	—	R
prasina s. str.			?			+		—	—	—	—
prasina s. lat.			?		+			—	—	—	—
prasina s. lat.			?				+	—	—	—	—
pycnidiophora			+					—	—	—	R
subleprosula	+							—	R	Y	—

Follmann (1972) who detected an unknown substance [= argopsin] in *Bacidia [Micarea] lignaria* [var. *lignaria*].

During my investigations a third of the 45 species of *Micarea* found in Europe have been shown to contain lichen substances (Table 2). Of the remaining 30 species the following have not been analysed by t.l.c. because the available specimens were too meagre: *M. contexta, M. intrusa, M. lithinella, M. melaeniza, M. melanobola,* and *M. rhabdogena*; however, spot tests on the thalli and apothecia in these specimens are all negative and the presence of lichen substances is unlikely, but not impossible.

Eight principal lichen substances are so far known in *Micarea*: alectorialic acid (including three or four accessory substances – ? derivatives), a depside of the β-orcinol series; argopsin, a depsidone of the β-orcinol series; gyrophoric acid, a tridepside of the orcinol series; two xanthones (not yet positively identified); and three unknown substances each found in different chemical races of *M. prasina*. The relative positions of these substances on chromatograms using solvent systems TDA and HEF are shown in Figs. 53 and 54.

Argopsin (1′ – chloropannarin) is found in *M. lignaria* var. *lignaria* and *M. leprosula*. It was originally isolated from *Argopsis friesiana* Müll. Arg. (belonging to the *Stereocaulonaceae*), and discussed at some length by Huneck & Lamb (1975). During the present investigation, and miscellaneous studies in collaboration with Mr P. W. James, it was found that this, then unknown, PD+ red substance in *M. lignaria* was identical to that in *Lecidea efflorescens* (Hedl.) Vainio and *Phyllopsora rosei* Coppins & P. James. A sample of *P. rosei* was sent to Dr J. A. Elix who identified the unknown substance as argopsin. This substance was found in several other species of *Phyllopsora* by Swinscow & Krog (1981), who referred to it as 'albicans unknown 2'.

The two unidentified xanthones are found together in *M. lignaria* var. *endoleuca*; more ample specimens of this variety are required for further chemical studies.

The most commonly encountered lichen substance in *Micarea* is gyrophoric acid, one of the

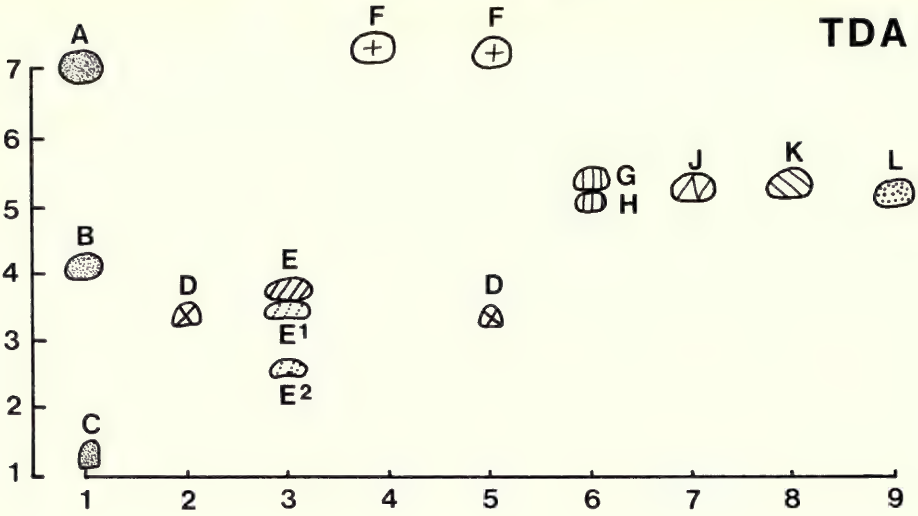

TDA
A
B
C
D
E
E1
E2
F
F
D
G
H
J
K
L
7
6
5
4
3
2
1
1
2
3
4
5
6
7
8
9

Fig. 53 Diagram of chromatogram in solvent system TDA.
1, Control (*Parmelia acetabulum* plus *Cladonia subcervicornis*). 2, *M. peliocarpa*. 3, *M. subleprosula*. 4, *M. lignaria*. 5, *M. leprosula*. 6, *M. lignaria* var. *endoleuca*. 7, *M. prasina s. lat.* 8, *M. prasina s. str.* 9, *M. prasina s. lat.* A, atranorin, B, norstictic acid. C, fumarprotocetraric acid. D, gyrophoric acid. E, alectorialic acid, and accessory substances (E^1, E^2). F, argopsin. G and H, xanthones. J, prasina unknown A. K, prasina unknown B. L, prasina unknown C.

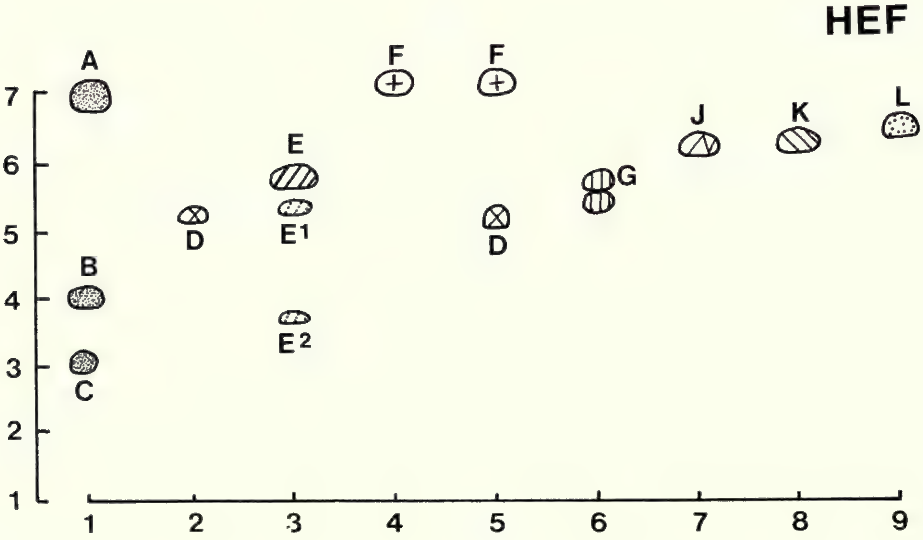

HEF
A
B
C
D
E
E1
E2
F
F
D
G
J
K
L
7
6
5
4
3
2
1
1
2
3
4
5
6
7
8
9

Fig. 54 Diagram of chromatogram in solvent system HEF.
Explanation as for Fig. 53.

most widely occurring compounds among lichen genera. It has been found in 11 *Micarea* species, although its presence in *M. curvata* has only been inferred from spot tests, the solitary specimen (holotype) being too small for t.l.c. analysis. In addition to these occurrences, gyrophoric acid is frequently detected in trace amounts in chromatograms of other taxa, especially *M. prasina s. ampl.* The fact that *Micarea* species often grow intermixed with other lichens, including several that contain gyrophoric acid (e.g. *Lecidea icmalea* and *L. granulosa* agg.) raises the question as to whether these trace amounts represent its presence as an accessory substance or as a contaminant. This is difficult to answer. Gyrophoric acid is certainly found in the *M. prasina* complex, as it has been detected in large amounts in the type material of *Lecidea levicula* Nyl. from Cuba. (Further studies are required to establish the taxonomic status of *L. levicula*.)

Well-developed specimens of *M. denigrata, M. nitschkeana*, and *M. melaena* have an areolate thallus containing readily detectable quantities of gyrophoric acid. However, the thallus of these species is sometimes scurfy-granular and blackish due to disruption by invading dematiaceous fungi and non-lichenized algae, and gyrophoric acid is produced in very low amounts or is apparently absent altogether (not detectable by t.l.c.).

The most surprising result of the chemical studies in *Micarea* was the discovery of three unknown, but very distinctive, compounds in *M. prasina*. The three compounds can be characterised thus (UV at 254 mμ):

prasina unknown A. TDA 5: HEF 6, UV+ blue-white. After H_2SO_4 and charring: UV+ dull orange-red, dull orange in daylight.

prasina unknown B. TDA 5: HEF 6, UV+ blue (less bright than 'unknown A'). After H_2SO_4 and charring: UV+ vivid citrine-yellow, yellow (without orange tinge) in daylight.

prasina unknown C. TDA 4–5: HEF 6–7 (slightly higher than 'unknowns A and B'), UV+ grey or pale mauve (TDA) or ± colourless (HEF). After H_2SO_4 and charring: UV+ violet-blue, ± colourless in daylight but turning a pale pinkish-lilac after several weeks.

In all the numerous European and North American specimens of *M. prasina s. ampl.* examined so far, these compounds have never been found in combination, and *M. prasina* exists as three distinctive chemical races (see taxonomic account of *M. prasina* for further discussion). None of the three compounds can be identified in the tabulations of Culberson (1972), and they have never been encountered in other genera during the numerous and diverse investigations by Mr P. W. James (pers. comm.). Samples of specimens containing 'unknowns A and B' are currently being studied by Dr J. A. Elix.

The identification of lichen substances (even if only by spot tests) is essential for distinguishing sterile specimens of *M. leprosula* from *M. subleprosula*, and for separating the two varieties of *M. lignaria*; it is also of great value in the routine identification of many other species (see 'Keys to species'). The three European races of *M. prasina* are not distinguishable by spot tests, but are readily identified by t.l.c.

Pigments

The nature of pigments and their location (especially within apothecia) are of prime importance in the delimitation of species within many lichen genera, particularly those included in the *Lecideaceae*, and *Micarea* is no exception. Little is known of these acetone insoluble pigments and a detailed knowledge of their structure and biogenesis would be invaluable for the evaluation of their taxonomic significance.

On the basis of the colours seen in water mounts and the colour changes brought about by the application of a strong alkali (KOH) and a strong acid (HNO_3) at least eight pigments can be recognized in *Micarea*. A very provisional summary of these pigments is given below:

Pigment A. Green or aeruginose, K− or + green intensifying, HNO_3+ red; in various tissues (according to species) of *M. assimilata, M. bauschiana, M. cinerea, M. intrusa, M. lignaria, M. melaena, M. peliocarpa, M. sylvicola*, and *M. tuberculata*.

Pigment B. Purple, K+ green, HNO_3+ purple-red; mostly in the hypothecium of *M. assimilata, M. contexta, M. crassipes, M. eximia, M. melaena, M. nigella*, and *M. sylvicola* (rare forms).

Pigment C. Purple, K+ purple intensifying (sometimes partly dissolving into solution); occasionally in the epithecium (*M. melaenida* and forms of *M. crassipes* and *M. melaena*) but mainly in the hypothecium (*M. assimilata, M. crassipes, M. melaena, M. melaenida*, and *M. subviolascens*).

Pigment D. Olivaceous, K+ violet (also C+ violet), HNO_3+ red; in various tissues (but rarely in the hypothecium, and then in low concentrations) of *M. denigrata, M. elachista* (mostly in pycnidia), *M. globulosella, M. hedlundii, M. melanobola, M. misella, M. nitschkeana, M. prasina, M. subviolascens*, and *M. synotheoides*.

Pigment E. Fuscous brown, K+ dissolving into solution, HNO_3−; in the epithecia of *M. elachista* and *M. rhabdogena*.

Pigment F. Brown (sometimes slightly tinged reddish), K− (not dissolving), HNO_3− or + orange-brown; in various tissues (according to species) of *M. botryoides, M. curvata, M. incrassata, M. lutulata, M. muhrii, M. myriocarpa, M. osloensis, M. subnigrata,* and *M. turfosa*. It is quite possible that more than one pigment is involved here.

Pigment G. Dilute yellowish, K+ purple (oily droplets), HNO_3−; in goniocysts and sometimes the lower hymenium and hypothecium of *M. hedlundii*.

Pigment H. Pale yellowish orange, K+ purple, HNO_3−; in cytoplasm of some ascogenous hyphae, asci, and spores of *M. intrusa*. This is possibly similar (or identical) to pigment G.

Pigment complexes involving mixtures of pigments A, B, and C are often found (especially in the hypothecium) in *M. assimilata, M. contexta, M. crassipes, M. melaena, M. subviolascens*, and *M. sylvicola*; see the individual species accounts for further details. The existence of such complexes suggests that pigments A, B, and C are closely related chemically.

Pigment A is probably identical to that found (usually in the epithecium) in a large number of lichens, especially in *Lecidea s. lat., Catillaria s. lat., Bacidia s. lat.* and *Lecanora s. lat.* Pigment C is probably of rare occurrence outside *Micarea*, but I know of it in the epithecium of *Bacidia beckhausii* and in several species of *Pertusaria* (e.g. *P. hymenea* and *P. oculata*). I have not encountered pigment E in any other lichens, but it should be compared with the pigment(s) responsible for the ionomidotic reaction found in several genera of non-lichenized discomycetes (Korf, 1973). Pigment F is probably of wide occurrence, but there may be several pigments that impart a brown or 'melanized' appearance in tissues.

The dark violet-blue, K+ aeruginose granules occasionally seen in the hymenium of *M. contexta* and *M. lignaria* (and also the apothecia of *Lecidea hypnorum* and *Dactylospora lobariella*), is probably related to (if not the same as) pigment B, and it may be the same as the epithecial pigment found in *Bacidia absistens, Mycoblastus fucatus*, and *Schaereria tenebrosa*.

Ecology

No detailed ecological studies have been made in connection with this primarily taxonomic study of *Micarea*, and much of the discussion given below is based on floristic notes and casual field observations. For most amateur and professional lichenologists alike, the species of *Micarea* are little known, poorly understood, and much overlooked in the field. For this reason the following account is more of a guide to collectors, rather than an ecological dissertation. Additional ecological notes are also included in the taxonomic accounts of each of the *Micarea* species treated. Syntaxonomic nomenclature follows James *et al.* (1977).

General habitats

Micarea species occur in a wide range of habitats but are confined to substrata with a low pH (below *c.* pH 5) and generally avoid nutrient enriched situations. Thus, they are absent from limestone rocks, tops of bird-perching stones, seashores, and basic bark. There are a few partial exceptions, for example *M. denigrata* can occur on wooden fencing and other timber in farmyards, *M. prasina* can occur on soil and debris among rocks in the upper seashore, and *M. lignaria* has been found on exposed limestone growing over mats or cushions of moribund bryophytes from which free calcium ions have presumably been leached out. The bark of *Acer* and *Ulmus* normally has a pH which is too high for species of *Micarea* (with the exception of *M. prasina* in some situations), but in areas heavily polluted by sulphur dioxide and its derivatives (e.g. West Yorkshire Conurbation), bark pH can be substantially lowered (Gilbert, 1970), thus providing a suitable substratum for species such as *M. melaena* (*q.v.*) and *M. botryoides* (*q.v.*).

The principal habitats (I–XI) in which *Micarea* spp. are found are given below; each is provided with a list of the species which can be expected to occur in it (allowing for climatic and phytogeographical variations). Species given in square brackets [ ] are rarely and unusually found in the given habitat, and those prefixed with a dagger (†) are not known in this habitat from the British Isles.

I. Sheltered, dry underhangs, usually in valley woodland or narrow ravines, including dry undersides of up-ended tree root systems in woodland; growing on rock, loose stones, consolidated soil, and exposed roots.
M. bauschiana
M. botryoides
M. lignaria
M. lutulata
M. myriocarpa
M. sylvicola
M. tuberculata

II. Exposed parts of sheltered rocks, usually in woodland; more frequently wetted than I; growing directly on rock.
M. botryoides
†*M. curvata*
M. lignaria s. lat.
M. lithinella
M. melaena
M. olivacea
M. peliocarpa
M. sylvicola
[*M. cinerea*]
[*M. denigrata*]
†[*M. muhrii*]
[*M. nitschkeana*][a]
[*M. prasina*]

a, stones amongst *Calluna* in heathland.

III. Over bryophytes on rocks, boulders, old stumps, or fallen trees in woodland at low altitudes (500 m in the British Isles).
M. adnata
M. botryoides
M. cinerea
M. leprosula
M. lignaria s. lat.
M. melaena
M. peliocarpa
M. prasina
[*M. stipitata*]

IV. Exposed, hard siliceous rocks; growing directly on rock.
M. intrusa
M. lignaria
M. subnigrata
†*M. subviolascens*
M. aff. *ternaria*[b]

b, coastal districts only.

V. Over bryophytes or peaty debris on exposed turf or on, or amongst, rocks and boulders in open situations in upland, montane, or 'arctic' districts.
M. assimilata
†*M. crassipes*
M. incrassata
M. leprosula
M. lignaria s. lat.
M. melaena
M. peliocarpa
M. subleprosula
†*M. ternaria*
M. turfosa
[*M. cinerea*]

VI. Over bryophytes or plant debris on the ground in old dunes, disused lead and zinc mines, sea-cliffs, or by woodland tracks.
M. botryoides
M. leprosula
M. lignaria s. str.
M. peliocarpa
M. prasina
[*M. denigrata*]
†[*M. misella*]

VII. On bare mineral soil at low altitudes.
†*M. melaenida*
†*M. osloensis*
[*M. leprosula*]
[*M. lignaria*]
[*M. prasina*]

VIII. Corticate trunks of healthy trees; usually in woodland; sometimes overgrowing bryophytes (*).
*M. alabastrites
*M. cinerea
*M. pycnidiophora
*M. stipitata

†_M. elachista_
†_M. globulosella_
M. melaena
†_M. melanobola_
*_M. peliocarpa_
*_M. prasina_
*_M. synotheoides_
[_M. botryoides_]
[_M. denigrata_]
[_M. leprosula_]
[_M. lignaria_]
[_M. nitschkeana_]

IX. On attached twigs of trees or large shrubs, or thin stems of small shrubs; in woodland, heathland, or scrub.

†_M. cinerea_
M. lignaria s. str.
M. nitschkeana
M. peliocarpa
M. prasina
[_M. denigrata_]

X. On timber (i.e. worked wood), e.g. fencing, garden furniture, old window frames, and shingles.

M. cinerea
M. denigrata
†_M. elachista_
M. lignaria s. str.
M. melaena
M. misella
M. nitschkeana
M. peliocarpa
[_M. globulosella_]
[_M. leprosula_]
[_M. sylvicola_]

XI. Directly on lignum of old stumps and decorticate trunks.

M. adnata
M. alabastrites
†_M. anterior_
M. cinerea
†_M. contexta_
M. denigrata
†_M. elachista_
†_M. eximia_
†_M. hedlundii_
M. lignaria s. lat.
M. melaena
†_M. melaeniza_
M. misella
†_M. muhrii_
M. nigella
M. nitschkeana
M. olivacea
M. peliocarpa
M. prasina
†_M. rhabdogena_
[_M. botryoides_]
[_M. leprosula_]
[_M. myriocarpa_]
[_M. synotheoides_]

From the above lists it will be seen that several species (e.g. *M. lignaria, M. melaena, M. peliocarpa,* and *M. prasina*) inhabit a very wide range of habitats and substrate. At the other extreme there are many species which are much more restricted e.g. *M. tuberculata* (I), *M. subnigrata* (IV), *M. assimilata* (V), *M. melaenida* (VIII), *M. pycnidiophora* (VIII), and *M. anterior, M. contexta, M. eximia*, and *M. melaeniza* (XI).

In most of the communities in which they occur *Micarea* species are usually of minor importance with regard to cover values. However, there are some exceptions such as the *Micareetum sylvicolae* association of underhangs and exposed tree root-system (see below), the community dominated by *M. prasina* on trunks in dense conifer plantations, some lignicolous assemblages on fallen trunks, old stumps, and worked wood. *Micarea nitschkeana* on *Calluna* twigs and litter in some lowland heaths, *M. melaena* on sandy or peaty soil in some heathlands and moorlands, and *M. lignaria* on the ground in some old lead mine workings.

Specific habitats

Deciduous (broad-leaved) woodland

In Britain the genus *Micarea* is best represented in terms of number of species per site in the mature, ± natural woodland (both deciduous and coniferous) on acid soils, in areas with a high annual rainfall (at least 1000 mm distributed over at least 160 'wet days'; see Coppins, 1976). The best examples of '*Micarea*-rich' deciduous (broad-leaved) woodlands are found in Wales, the English Lake District and the west of Scotland north of the Clyde Estuary. The *Micarea* species found in them on trees and stumps are included in lists III, VII, and XI above, except that *M. misella, M. nigella,* and *M. olivacea* are primarily species of coniferous woodlands.

The occurrence of *Micarea* spp. on bark (or over bryophytes thereon) is favoured by leaching, and is further favoured, to the detriment of more basicolous lichens, by the effects of 'acid rain'

(Anon, 1980; Fowler *et al.*, 1982). Acid rain effects, resulting from the pollution emitted from the industrial areas of west-central Scotland (Clydeside and Glasgow conurbation), are probably the explanation for the prevalence on the trunks of mature trees (e.g. *Quercus, Alnus, Betula,* and *Fraxinus*) of such species as *M. alabastrites, M. cinerea, M. peliocarpa, M. stipitata,* and *M. synotheoides* in the deciduous woodlands of the Cowal Peninsula in southern Argyllshire. The communities in which these species occur are probably referable to the *Parmelietum laevigatae*, and in areas subjected to 'acid rain' it appears that these communities have to some extent, and in certain situations (especially on *Quercus* and *Fraxinus*), replaced the more basicolous communities of the *Lobarion pulmonariae*.

In the deciduous woodlands of drier parts of the British Isles (annual rainfall of <1000 mm over <160 'wet days') *Micarea* species are less prevalent on the trunks of healthy trees, and *M. prasina* is the only species commonly encountered, although *M. nitschkeana* can often be found on twigs and thin branches. However, *M. peliocarpa* is occasionally found growing amongst (but not on) mosses on the bark of old *Quercus* trunks in ancient woodlands, especially in the New Forest, Hampshire. Similar occurrences of *M. peliocarpa* are known from the old oak-woods of north Jylland in Denmark, and north-west France.

Coniferous woodlands

The formerly extensive native Caledonian pine-forest of Scotland is now reduced to a few scattered relics totalling about 10050 ha (26000 acres), of which only about 1620 ha (4000 acres) is represented by dense stands of *Pinus sylvestris* (Steven & Carlisle, 1959; Goodier & Bunce, 1977). These woodlands cannot be described as 'natural' because they have all been managed commercially to some extent during the last 200 years. Nevertheless, most of them contain many old trees, together with standing and fallen decorticate trunks, and are rewarding sites for the seeker of *Micarea* species. From the analysis of various vegetational and edaphic characteristics, the Scottish native pinewoods can be divided into four 'site types' (Bunce, 1977). The *Micarea* species recorded by me from some of the pinewoods in three of these site types are listed in Table 3. This indicates a poor *Micarea* flora for the eastern site type which is probably due to their lower rainfall. However, it is in these eastern (Speyside and Deeside) pinewoods where special efforts should be made to search for the group of lignicolous species (*M. anterior, M. contexta, M. eximia, M. melaeniza, M. muhrii,* and *M. rhabdogena*) which are so far known only from the coniferous forests of Scandinavia (especially mid-Sweden). To these can be added the more widely distributed *M. elachista* and *M. hedlundii*.

An ever increasing proportion of British woodland (especially in Northumbria and Scotland) is composed of densely planted evergreen conifers such as *Picea sitchensis, P. abies, Pinus sylvestris*, and to a lesser extent other species including *Abies grandis, A. procera, Pinus contorta,* and *Pseudotsuga menziesii*. In some old plantations (70+ years) in the central and western Scottish highlands species of *Micarea* (including *M. alabastrites, M. cinerea, M. peliocarpa, M. stipitata,* and *M. synotheoides*) may colonise the trunks of mature trees, particularly in less-shaded situations by forest tracks and fire-breaks. However, most of the commercial forests contain closely planted trees less than 30 years old, and the light regime in such forests is so poor that it ± prohibits the development of both a ground flora and an epiphyte flora of tree boles. The most successful lichen in these deeply shaded situations is the ubiquitous *M. prasina* which occurs in them as a form with a thinly developed thallus and small, whitish (translucent when wet) apothecia; in this form it is easily overlooked as a thin dark green algal-scum covering trunks and fallen branches. Old stumps in dense plantations sometimes also support *M. melaena* and the newly described *M. nigella* (*q.v.*).

Larix is another frequently planted conifer, but because it is deciduous, its trunks are soon colonised by photophilous communities of the *Pseudevernietum furfuraceae* and *Usneion barbatae*. These communities are dominated by foliose and fruticose lichens, thus leaving little available space for crustose species, although species such as *M. melaena, M. peliocarpa,* and *M. prasina* are sometimes present in small quantities. On the other hand, the long slender twigs of *Larix* are commonly colonised by *M. nitschkeana*, often accompanied by *Scoliciosporum chlorococcum*, so forming communities referable to the *Bacidietum chlorococcae*.

Saxicolous habitats

Of the 45 European species of *Micarea*, 21 have been found growing directly on rock (lists I, II, and IV), although the genus is poorly represented in the main saxicolous lichen alliances of exposed siliceous rocks (e.g. *Lecideion tumidae, Rhizocarpon alpicolae*, and *Umbilicarion cylindricae*; list IV). As saxicoles *Micarea* species are more prevalent in sheltered ravines and woodlands. In dry underhangs in rock faces, steep banks, and below overhanging trees, up to seven species (list I) may be found in the ombrophobous, aerohygrophilous *Micareetum sylvicolae*. The species in this community grow on rock, loose or lodged stones, exposed roots, consolidated soil, and encroaching dry mats of bryophytes. Associated lichens from other genera may include *Coniocybe furfuracea, Enterographa hutchinsae, Melaspilea subarenacea, Microcalicium arenarium, Opegrapha gyrocarpa, O. zonata, Porina chlorotica, P. lectissima, Psilolechia clavulifera*, and *P. lucida*. This community is usually well defined, but in some situations it intergrades with other assemblages of shaded rocks such as the *Lecideetum lucidae, Coniocybetum fururaceae, Opegraphetum horistico-gyrocarpae,* and the *Racodietum rupestris*.

A few *Micarea* species (list II) may be found on the upper sides of stones, boulders, and rocks where they are subjected to direct wetting by rain, or by drips from the overlying tree canopy. In most cases these are incidental occurrences of species more characteristic of other substrata. However, such situations may be the normal habitat of the little known *M. curvata* and *M. lithinella*.

In northern and western Britain several *Micarea* species occur on mossy rocks. The communities involved are often difficult to place, some belonging to bryophyte-dominating syntaxa, others to normally epiphytic communities (e.g. *Parmelietum laevigatae*), or to chomophytic communities dominated by bryophytes and *Cladonia* species which, in turn, are often invested by a gelatinous algal scum.

Terricolous habitats

Areas of lowland heathlands where the peaty or sandy soil has been laid bare of tall vegetation by erosion, disturbance, or burning are colonised by several species of algae bryophytes and lichens. The lichens involved often include species such as *Lecidea icmalea, L. uliginosa, L. oligotropha* (rare in Britain), *Baeomyces rufus, B. roseus*, and some *Cladonia* spp. *Micarea* species are not usually involved in such communities, although *M. melaena* may at times be present, occasionally achieving local dominance. In mature *Callunetum* in the heathlands of eastern England and Jylland (Denmark) *M. nitschkeana* is sometimes encountered in abundance on litter, as well as on the thin attached twigs of the *Calluna*. Acidic soils contaminated by heavy metals (especially lead) are often rather bare with an open vegetation, and *Micarea* species (especially *M. lignaria*) may occur in quantity growing over moribund bryophytes and plant debris. Soil, plant debris, and moribund bryophytes amongst coastal rocks are often colonized by *M. prasina* (*q.v.*). *M. melaenida* (*q.v.*) is found exclusively on consolidated fine grained (argillaceous) mineral soils. The terricolous species encountered in upland, montane, or arctic regime are given in list V; the reader is referred to the individual species accounts for further details.

Man-made substrata

A detailed treatment of the lichens of man-made substrata is given by Brightman & Seaward (1977). Several *Micarea* species occur on worked wood (list X), but *M. denigrata* (*q.v.*) is by far the most successful species. *M. denigrata* has also been found on pieces of hardboard lying in a dune slack at Tentsmuir in Fife. Old sackcloth and other fabrics lying on the ground in old lead-mine workings are frequently colonised by lichens, including *M. lignaria*. A more surprising find was that of *M. nitschkeana*, growing with *Scoliciosporum umbrinum*, on a small plastic carton in a heathland on the Isle of Wight. Further field studies will undoubtedly extend this list of artificial substrata. *Micarea denigrata* and *M. prasina* are rapid colonisers of newly available substrata, and have been collected respectively on dead culms of *Cladium mariscus* and *Phragmites australis* in natural habitats. Both of these reeds are sometimes used as thatch, and a close inspection of thatched roofs ought to reveal the presence of *Micarea* species.

Habitats in lowland pastoral areas

The lowlands of eastern England, the English south midlands and parts of eastern Scotland contain few 'natural' habitats suitable for *Micarea* species. In addition, these same areas suffer, at least to some extent, from the effects of incoming pollution (especially sulphur dioxide and its derivatives) and indigenous pollution in the form of agricultural biocides and fertilisers. Nevertheless, the diligent collector will usually discover suitable niches where *Micarea* species are to be found. The most commonly encountered member of the genus in lowland agricultural and suburban districts is *M. denigrata* which can grow on worked wood in a wide range of situations, and on old tree stumps in hedgerows. *M. prasina* can be found on trees and shrubs in small woodlands planted as fox coverts or for the rearing of pheasants. It may also be found on sheltered stems of shrubs in waste ground, marginal land, or gardens, where *M. nitschkeana* may also occur.

A major refuge for wildlife (including lichens) in lowland Britain is provided by churchyards (Anon, 1973, 1978). Although records of *Micarea* species are rather few, *M. denigrata* can often be found on timber and, more rarely, on siliceous memorial stones; and *M. lignaria* and *M. peliocarpa* have been recorded on the siliceous stone-work of old walls and memorials.

Distribution

Britain

Maps 1–28 present the distributions of all the *Micarea* species occurring in the British Isles, with exception of *M. lithinella* which is known from just one 10 km grid square (44/86). It is seen from these maps that records for most species are concentrated in the western and/or northern districts. This is partly due to the fact that suitable habitats are most numerous in these areas, and it is probable that several species (e.g. *M. bauschiana, M. lignaria, M. melaena, M. peliocarpa,* and *M. sylvicola*) would be more evenly distributed if there were more available habitats in the lowland areas of the south and east. It is impossible to discuss in isolation the effects of climate or substrate availability on plant distributions. Substrate availability is largely dependent on topography and geology, but the physical and chemical nature of an existing substratum can be much influenced by the prevailing climate. For example, the bark of trunks of mature *Quercus* in high rainfall districts tends to be more leached, soft, and friable (i.e. more suitable for *Micarea* spp.) than in low rainfall districts. As a second example the species of the *Micareetum sylvicolae* (see p. 92) are ombrophobous (avoid frequent direct wetting), but are also aerohygrophilous (require ± constant high humidity). In western Britain the high rainfall, high incidence of cloud cover (i.e. low duration of possible sunshine), and incoming moist air-stream from the Atlantic on the prevailing westerly winds result in high levels of relative humidity (and low levels of saturation deficit) more or less throughout the year (see *Climatological Atlas of the British Isles,* London: HMSO (1952)). Under such conditions a well developed *Micareetum sylvicolae* can be found on underhangs in a wide range of lowland habitats. Eastern districts generally have a lower rainfall and lower incidence of cloud cover resulting in lower levels of relative humidity, such that the *Micareetum sylvicolae* tends to be more confined to narrow river valleys with a long history of continuous tree cover. A western bias to the present day British distribution of many lichens is often due to the fact that the eastern side of the country is generally that most affected by industrial and urban development, intensive agricultural practices, and the resultant forms of air pollution (Hawksworth, Coppins & Rose, 1974; Coppins, 1976).

A climatically determined western distribution, attributable to the General Western Group of Coppins (1976), is shown by *Micarea adnata, M. alabastrites, M. cinerea, M. lignaria* var. *endoleuca, M. stipitata,* and *M. synotheoides*. These species have a eu-Atlantic or sub-Atlantic European distribution, and are confined to areas with an annual rainfall of over 800 m (mostly over 1000 mm) distributed over at least 160 wet days ['wet day' = period of 24 h in which 1 mm (or more) of rain is recorded]. The genus *Micarea* is poorly represented in southern (Mediterranean) Europe, and it is not surprising that few British species exhibit a marked southern tendency. The best example of such a species is *M. pycnidiophora*, which is mainly confined to

Table 3 Distribution of *Micarea* species in some of the site types of Scottish native pinewoods.

	SITE TYPE SW	 C	 E
Annual rainfall (mm)	2000–2800	1300–1800	760–1150
lignaria var. *endoleuca*	+	—	—
stipitata	+	—	—
adnata	+	+	—
alabastrites	+	+	—
lignaria var. *lignaria*	+	+	—
synotheoides	+	+	+
melaena	+	+	+
peliocarpa	+	+	+
prasina	+	+	+
cinerea	—	+	—
nigella	—	+	—
nitschkeana	—	+	—
misella	—	+	+

Site types are according to Bunce (1977). The woods studied (with 10 km grid-references) are as follows. *South-western* (SW): Barisdale (18/80); Black Mount Woods (27/24 & 27/34). *Central* (C): Black Wood of Rannoch (27/55); Glen Affric (28/12 and 28/22); Glen Moriston (28/31); Glen Strathfarrar (28/33); Guisachan Forest (28/22). *Eastern* (E): Abernethy Forest (38/01); Rothiemurchus Forest (28/90).

the New Forest, and its British distribution reflects its overall southern eu-Atlantic distribution, although it appears to avoid areas with an extremely high rainfall. A markedly eastern distribution is not clearly exhibited by any of the well known British species, although *M. nitschkeana* appears to occur with greater frequency and in greater abundance outside of the predominantly western areas with a very high rainfall.

Amongst the species of low altitude habitats (mostly <500 m) a distinctly northerly distribution (not related to high rainfall) is best exemplified by *M. misella*. The arctic-alpine species of *Micarea* have a northern distribution, and are apparently confined to Scotland. One possible exception is the little known *M. subleprosula* with its single British locality in north Wales. However, this species has probably been overlooked, and I believe it to be just a matter of time before it is recorded from Scotland.

The most widely and evenly distributed species of *Micarea* in Britain are *M. denigrata* and *M. prasina*; both are efficient colonisers of a wide variety of newly available substrata, even in areas of suburban development and intensive agriculture. The dearth of records of common species in Ireland is due to under-recording.

Europe

An accurate assessment of distribution patterns exhibited by such little known and poorly understood organisms as members of the genus *Micarea* is likely to be an impossible task for many years. Distributions can be easily misinterpreted due to uneven recording. Many large areas may be underworked (or not studied by all) by collectors familiar with the group concerned, and other areas may be, by contrast, intensively studied. Consequently, when analysing the resultant records there is always the danger of artificially creating 'centres', 'headquarters' or trends of distribution. This state of recording is applicable at the present time to *Micarea* species, which are best known in mainland Britain, the southern halves of Norway, Sweden, and Finland, southern Bavaria and the Schwarzwald (Black Forest), Austria, the Italian Tirol, and the Sudety and Carpathian Mts of Czechoslovakia. It is probably safe to generalise that these areas have, coincidentally, the highest concentrations of *Micarea* species. However, field studies are required to determine which *Micarea* species are present in other potentially rich areas which are as yet little studied. These areas include Bretagne, south-east France, the Pyrénées, Cantabrian Mountains, northern Apennines, Dinaric Alps, southern Carpathians, Transylvanian Alps, Balkan Mountains, and the Rhodope Mountains.

The identification (and subsequent annotation and cataloguing) of a single specimen of _Micarea_ (which more often than not is fragmentary or in poor condition) can be very time consuming, and often involves lengthy microscopical examination. The unfortunate consequence of this is that I have not been able to examine a large number of potentially available specimens from several major institutional and private herbaria.

Despite the above problems and shortcomings, I have tentatively attempted below to assign the species of _Micarea_ to some general distributional types. In most cases I have paid little attention to purely literature sources of records because I have found that many such reports, even those by lichenologists whose works I hold in the highest esteem, can be unreliable in respect of current species concepts.

A. Eu-Atlantic – mainly confined to oceanic areas including west Norway, the British Isles, western France, and Macaroenesia.

M. alabastrites
M. nigella
M. olivacea
*_M. prasina_ (with 'unknown C')
*_M. pycnidiophora_
*with southern tendency

M. stipitata
M. subnigrata
†_M. subviolascens_
M. synotheoides
†with affinity to group G

B. Sub-Atlantic – as above, but also present in high rainfall (annual rainfall of >800 mm) areas of central Europe (Alps, Carpathians, etc.).

M. adnata
M. cinerea
M. lignaria var. _endoleuca_

C. Boreal – mainly confined to Fennoscandia, but absent or rare from west Norway.

M. anterior
M. contexta
M. eximia
M. melaeniza
M. melanobola
M. muhrii
M. osloensis
M. rhabdogena

D. Boreal-continental – present in Fennoscandia and central Europe, but rare or absent from west Norway and western Britain.

M. elachista
M. hedlundii
M. lithinella
*_M. melaenida_
*but known from western France

E. Continental – known only from central Europe.

M. curvata

F. Montane (arctic-alpine) – at high altitudes in montane regions of Britain and central Europe, but sometimes at low altitudes in Fennoscandia.

M. assimilata
M. crassipes
M. incrassata
M. subleprosula
M. turfosa

G. Arctic – mainly confined to within the Arctic Circle, but possibly extending southwards along the Atlantic coast.

M. ternaria

H. Widely Distributed – known from British Isles, Fennoscandia, central Europe, and often elsewhere. More records will probably reveal distinct phytogeographical tendencies for some of the species included here.

M. bauschiana
M. botryoides
M. denigrata
‡_M. globulosella_
M. intrusa
M. leprosula
M. lignaria var. _lignaria_
M. lutulata
M. melaena
†_M. misella_
M. myriocarpa
M. nitschkeana
‡_M. peliocarpa_
*_M. prasina_
M. sylvicola
M. tuberculata
*races containing 'prasina unknowns A and B'
†with possible affinity to group D
‡with possible affinity to group B

World

The present study is confined to species of *Micarea* that occur in Europe. However, some extra-European specimens have been examined in connection with nomenclatural matters, and others have been examined incidentally. According to current information the genus is best represented in Europe, but this may, or may not, be true. *Micarea* is well represented in North America from where I have seen 12 species (all European taxa: *M. crassipes, M. denigrata, M. globulosella, M. lignaria s. str., M. melaena, M. misella, M. nitschkeana, M. peliocarpa, M. prasina, M. sylvicola, M. ternaria*, and *M. turfosa*); this list will undoubtedly be much extended in the near future. From other regions I have seen (but not necessarily critically examined) specimens of *Micarea* from Japan, Borneo, Tasmania, New Zealand, South Africa, South America (Brazil), and the Antilles (Cuba). It is likely that species of *Micarea* are to be found in most temperate and boreal regions, as well as in many tropical regions (especially mountainous areas). The numerous collections that I have received from New Zealand include several undescribed taxa but they also include at least one European species, *Micarea peliocarpa.* Three additional European species known from the southern hemisphere are *M. incrassata* (Kerguelen), *M. lignaria* (Brazil), and *M. misella* (Brazil).

The genus *Micarea*

Micarea Fr.

Syst. orb.: 256 (1825). – *Micarea* Fr. emend Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18**(3): 27 (1892). Lectotype: *Micarea prasina* Fr. (see note below).

Helocarpon Th. Fr., *Lich. arctoi*: 178 (1860); *Nova Acta R. Soc. Scient. Upsal.* III, **3**: 278 (1861). Type species: *Helocarpon crassipes* Th. Fr. [= *Micarea crassipes* (Th. Fr.) Coppins].

Stereocauliscum Nyl. in *Flora, Jena* **48**: 211 (1865). Type species: *Stereocauliscum gomphillaceum* Nyl. [= *Micarea lignaria* (Ach.) Hedl.]

Micarea sect. *Bryophagae* Poelt & Döbbeler in *Bot. Jb.* **96**: 337 (1975). Type species: *Micarea polytrichi* Poelt & Döbbeler [= *Micarea prasina* Fr.].

Note. The name *Micarea* was first validly published in December 1825 by Fries (*op. cit.*), although it was twice mentioned by the same author earlier in the same year. In *Sched. crit. lich. suec.* part 3, fasc. 4, page 21 (pre 7 May) it appeared in a note under the entry for *Biatora fuliginea*. However, it was not accepted in that work, and must therefore be considered invalid according to Art. 34.1. The second appearance was in *Stirp. agri. femsion.* page 37 (June 1825) in the form of the combinations '*Micarea fuliginea*' and '*M. nigra*'. Neither of these was accompanied by a description and the generic name was again invalidly published (Arts 32, 34.1(e)).

When validly published, *Micarea* was introduced with four species: *M. prasina, M. coccinea, M. fuliginea,* and *M. nigra*. Körber (1855) emended the genus to include only *M. prasina* and is thereby considered to have lectotypified the genus on that species. See 'Excluded taxa' for notes on the remaining three original names.

Thallus crustose or immersed in the substratum, effuse and often wide-spreading, never bordered by delimiting hypothalline lines. Superficial thallus consisting of ± spherical granules (goniocysts) up to *c.* 60 ±m diam; or convex to subglobose areolae which in some species may dissolve into soredia: or more rarely present as a thin ± smooth to rimose, or scurfy-granular crust. Thallus in section ecorticate (or weakly corticate in a few species), but sometimes (when areolate) covered by a hyaline amorphous layer, and outermost hyphae sometimes pigmented. *Phycobiont* 'grass-green'; cells usually thin-walled and *c.* 4–7 μm ('micareoid'), or more rarely larger ('non-micareoid' phycobiont types); a few species also have *cephalodia* containing *Nostoc* or *Stigonema*.

Apothecia small (mostly <1 mm diam), whitish or variously coloured (mostly grey, dull brown or blackish), epruinose, usually immarginate or ± so, adnate, sessile or rarely stipitate, convex to ± globose and often becoming tuberculate. *Hymenium* with amyloid gel-matrix. *Asci* clavate or cylindrical-clavate, of *Lecanora*-type, 8-spored. *Spores* hyaline, smooth-walled, variously shaped (ellipsoid, ovoid, fusiform, or acicular), usually less than 6 μm wide, simple to multiseptate but never muriform. *Paraphyses* few to numerous, septate, mostly branched (especially above), often anastomosing, mostly in range of 0·7–1·7 μm wide at mid-hymenium;

apices never regularly clavate or capitate and never with a dark brown apical 'cap', but sometimes irregularly incrassate and sometimes with thickened pigmented walls in about upper 5–15 μm; in addition, some species have a few stout paraphyses (which are *c.* 2–3 μm wide, and, in some cases, pigmented throughout their length) occurring as scattered individuals or small fascicles. *Hypothecium* (including subhymenium) variously pigmented, of interwoven hyphae that become outwardly orientated towards the hymenium, mixed with wider, short-celled ascogenous hyphae. *Excipulum* often absent or indistinct, if discernible then non-amyloid (or ± so) and composed of radiating branched and anastomosing paraphysis-like hyphae that become distinct and ± separate in K.

Pycnidia often present, very varied in form from immersed to sessile or stalked, the stalks (pycnidiophores) sometimes branched. Pycnidial walls hyaline or pigmented. *Conidiogenous cells* ampulliform to cylindrical (sometimes with swollen base), phialidic, sometimes with 1–3 proliferations. *Conidia* hyaline, smooth-walled, of three basic types: (i) *microconidia* – ± cylindrical, aseptate, eguttulate, in range 3·5–9×0·5–1 μm, borne in immersed to sessile pycnidia usually <50 μm diam; (ii) *mesoconidia* – cylindrical, ellipsoid, obvoid or ovoid-oblong, aseptate, often biguttulate, sometimes constricted in the middle, mostly in range 2·8–8× 1–2 μm, borne in immersed, emergent, sessile or stalked pycnidia mostly in the range 30–200 μm diam; (iii) *macroconidia* – curved, hamate or filiform or rarely helicoid, often septate, *c.* 1–1·5 μm wide, borne in immersed to ± sessile pycnidia mostly in the range 50–300 μm diam.

Sporodochia known in one species, producing large oblong-ellipsoid macroconidia on long, slender conidiogenous cells.

Chemistry various, several species with gyrophoric acid in apothecia and pycnidia, and (or) thallus; alectorialic acid, argopsin, two xanthones, and at least three unknown substances have also been found; many species are without lichen substances.

Intergeneric considerations

The genus *Micarea* as emended by Hedlund incorporates species with crustose thalli, biatorine or lecideine apothecia, and hyaline, simple or transversely septate spores; these species have been (or would have been) placed in *Lecidea* Ach., *Catillaria* Massal., or *Bacidia* de Not. according to the systems of Zahlbruckner (1921–40, 1926). However, the type species of these genera (*viz. L. fuscoatra* (L.) Ach., *C. chalybeia* (Borrer) Massal., and *B. rosella* (Pers.) de Not.) all have an excipulum composed of coherent hyphae which do not become lax in K and do not closely resemble paraphyses. Similarly, a more complex ('advanced') excipulum structure than that characteristic of *Micarea* is also found in several recently re-established or newly described crustose genera of the *Lecideaceae* s. str., e.g. *Biatora* Fr. (non Ach.), *Biatorina* Massal., *Cliostomum* Fr., *Herteliana* P. James, *Huilia* Zahlbr., *Lecidella* Körber, *Melanolecia* Hertel, *Tremolecia* Choisy, and *Tylothallia* P. James & Kilias. *Fuscidea* V. Wirth & Vězda and *Rhopalospora* Massal. could be added, but they should be excluded from the *Lecideaceae* on account of their asci which appear to belong to the *Teloschistes*-type.

The genus most closely resembling *Micarea* appears to be *Scoliciosporum* Massal., whose species have fusiform-acicular, sigmoid, or vermiform spores. In the main, species of both genera have small, immarginate apothecia, a basically simple thallus structure, ± clavate asci of the *Lecanora*-type, frequently branched paraphyses, and an excipulum of paraphysis-like hyphae. The type species of *Scoliciosporum* (*S. umbrinum* (Ach.) Arnold) is sometimes seen to have some paraphyses terminating in swollen apices, each provided with a dark pigmented 'cap'. This feature is common in well developed specimens, but may be difficult or impossible to see in abraded or shade forms. I have also observed apical 'caps' in *S. chlorococcum*, although they may not necessarily be found in all the other species included in the genus by Vězda (1978) and Poelt & Vězda (1981). I have not found them in *S. pruinosum*, but that species has an epithecium containing dense, minute granules which dissolve in K. To my knowledge, no species of *Scoliciosporum* has lichen substances or a 'micareoid' phycobiont, and most (if not all) of the species rarely (if ever) produce an anamorphic (conidial) state(s). The opposite situation in the cases of all three of these features is not common to every species of *Micarea*, but is true for most species in at least one case. *Micarea intrusa* (*q.v.*) possibly provides a link between the two genera, and its inclusion in *Micarea*, rather than *Scoliciosporum*, is mainly on the grounds of spore-type. The differences between the two genera are admittedly unclear and ill-defined at the present time, and will certainly require re-appraisal as our knowledge of morphological, ontogenetic, and phylogenetic aspects in the *Lecideaceae* increases.

A genus which may be closely related to both *Micarea* and *Scoliciosporum* is *Strangospora* Massal.; it shares with them unsophisticated apothecial and thallus structures, and similar ecological requirements. However, *Strangospora* differs in having polysporous asci with aseptate, globose spores, although the asci do appear to be of the *Lecanora*-type. The monotypic genus *Steinia* Körber is represented by *S. geophana* (Nyl.) Stein, whose small, black, immarginate apothecia occurring on shaded substrate (soil, rotten wood, rocks, stones, etc.) are easily confused in the field with those of some *Micarea* species. However, it is easily distinguished in microscopical preparations by its 16-spored asci with globose spores, and simple, slender paraphyses. In addition, its asci are not of the *Lecanora*-type, although their apices are each provided with a broad, amyloid plug.

Micarea appears to have some affinities to *Psilolechia* Massal., and the two genera are compared in the discussion of *Psilolechia clavulifera* (p. 376). *Micarea* may also be close to the predominantly foliicolous *Byssoloma* Trevisan, but species of this latter genus have an excipulum of loosely woven, hyaline, pachydermatous hyphae which spread laterally to form a conspicuous white border to the apothecium. However, some specimens of *B. subdiscordans* (Nyl.) P. James, when growing on bark, mosses, or rocks, do not have conspicuous white-bordered apothecia, although the pachydermatous hyphae are clearly seen in sections of the apothecia.

Lignicolous members of the *'Lecanora' symmicta* group are occasionally confused with *Micarea* species on account of their general appearance and excipulum structure. Their excipular hyphae are radiating, richly branched and anastomosed and lax in K, although they contrast markedly with the simple or sparingly branched paraphyses and do not give the impression of being 'paraphysis-like'. This group further differs from *Micarea* in having dense epithecial granules which dissolve in K and a generally different suite of lichen substances (which includes usnic acid and zeorin). Another seemingly distinctive group of species (but not yet afforded generic status) that bears some close resemblances to *Micarea* is that containing such species as *Catillaria contristans, Lecidea limosa,* and *L. stenotera*; for further discussion see account of *Micarea assimilata* (p. 115).

The apothecia of *Vezdaea* species are superficially similar to those of some species of *Micarea*, but differ in that their tissues are not bound by a gelatinous matrix and their asci have uniformly amyloid walls and do not belong to the *Lecanora*-type; see Poelt & Döbbeler (1975).

There has been some confusion between *Micarea* and genera such as *Arthonia* Ach., and *Chrysothrix* Mont., and also the *Trapelia*-like *'Lecidea' granulosa* group. These all differ from *Micarea* in not having *Lecanora*-type asci (see 'Excluded taxa').

Suprageneric considerations

The formulation of a ± stable hierarchical classification of fungal (including lichen) taxa above the rank of genus is unlikely to be achieved for some decades. A suprageneric classification for the lichenized fungi has been attempted in recent years by, for example, Henssen & Jahns (1973) and Poelt (1974*b*). These schemes are extremely useful bases for further study but, as admitted by their authors, contain very many uncertainties and points of conjecture, and should be regarded as being of a very provisional nature.

Micarea has *Lecanora*-type asci and clearly belongs in the order Lecanorales and suborder Lecanorineae as defined by Poelt (1974*b*). My belief is that *Micarea* should be placed in the *Lecideaceae* Chev. *s. str.* (i.e. confined to species with *Lecanora*-type asci), with the provision that the real differences (if any) with that family and the *Lecanoraceae* Fée need to be explored. For the time being (at least) I cannot accept the 'Micareaceae Vězda ad int.' (Poelt, 1974*b*: 627; Eriksson, 1981), although it may be possible to formally define this family name in the future as knowledge and taxonomic concepts in the Lecanorales increases and advances.

Infrageneric considerations

I have given much thought to the possibility of subdividing the genus *Micarea* into subgenera or sections. The genus includes several small groups of closely related species, but the affinities of many individual species are difficult to ascertain. I believe that a formal infrageneric classification (above the rank of species) based on current information would be unlikely to withstand the tests of time and serve little useful purpose. However, that is not to say that such a classification will never be possible. The present study is mainly confined to the 45 European species of *Micarea*, but the genus is well represented in other parts of the world by some of the same, plus numerous additional species. With such considerations in mind I estimate that the genus, as currently circumscribed, contains about 100 species world-wide. A better understanding of extra-European species may increase the feasibility of subdividing *Micarea*.

Some examples of small groups of apparently closely related species are given below. Within each group all the species have basically similar apothecial construction. For example, Group C all have medium to large sized apothecia, a ± well-developed excipulum, and numerous paraphyses which are of medium thickness and are richly branched (especially in the upper hymenium). Some supplementary common features and other notes are provided for each group – but for more detailed discussions see the taxonomic accounts of the relevant species. Phycobiont is 'micareoid' unless otherwise stated. See under 'Chemistry' for explanation of pigments. Abbreviations: AL, hyaline amorphous covering layer; Exc., excipulum; Hym., hymenium; Hyp., hypothecium; Th., thallus; Pyc., pycnidia.

A. *M. lignaria – M. ternaria*
Th. areolate-type with AL. Th., Hym. and Pyc. with pigment A; Hyp. with dilute pigment A plus dilute dull brown pigment. Spores ± fusiform, 3- or more septate. Mesoconidial states very similar; *M. lignaria* also has micro- and macroconidial states. Chemistry: argopsin or xanthones (*M. lignaria*) or no substances (*M. ternaria*).

B. *M. leprosula – M. subleprosula*
Th. sorediate-type. Th. and Hym. with pigment A; Hyp. often with dilute dull brown pigment. Spores ± fusiform, 3- or more septate. Anamorphs unknown. Chemistry: argopsin + gyrophoric acid (*M. leprosula*) or alectorialic acid + accessory substances (*M. subleprosula*). Many affinities with Groups A and C.

C. *M. peliocarpa – M. alabastrites – M. cinerea*
Th. areolate-type with AL. Hym., Th. and Pyc. of *M. peliocarpa* and *M. cinerea* with pigment A; all parts of *M. alabastrites* devoid of pigment. Spores ± fusiform, 3- or more septate. All with microconidia and curved or filiform macroconidia; mesoconidia unknown. Chemistry: all with gyrophoric acid. With Atlantic or sub-Atlantic distributions. Some affinities with Groups A, B, and D.

D. *M. denigrata – M. nitschkeana – M. globulosella*
Th. areolate-type but with no AL. Hym., Th. and Pyc. with pigment D; Hyp. hyaline. All with similar micro- and mesoconidial states; *M. denigrata* and *M. nitschkeana* also with ± identical macroconidial states. Chemistry: all with gyrophoric acid. Mainly corticolous or lignicolous. These three species appear to show a good example of an evolutionary progression: they are morphologically and chemically ± identical except for the length and septation of spores.

E. *M. pycnidiophora – M. stipitata*
Th. areolate-type, but with no AL. Without pigments. Spores ± acicular, 3–7-septate. Pyc. stalked, with mesoconidia; micro- and macroconidia unknown. Chemistry: gyrophoric acid (*M. pycnidiophora*) or no substances (*M. stipitata*). Corticolous and with eu-Atlantic distributions.

F. *M. elachista – M. rhabdogena*
Th. areolate-type with cortex and AL (*M. elachista*) or endoxylic (*M. rhabdogena*). Upper Hym. with pigment E; Pyc. with pigment D; Hyp. hyaline. Macroconidia unknown. Chemistry: no substances. Mainly lignicolous with boreal or boreal-continental distribution.

G. *M. botryoides – M. melaeniza*
Th. weakly areolate (with no AL) or with goniocysts (*M. botryoides*), or endoxylic (*M. melaeniza*). Hym. and Pyc. walls with pigment A; Hyp. and Pyc. stalks with pigment F. Paraphyses dimorphic. Pyc. stalked with mesoconidia; micro- and macroconidia unknown. Chemistry: no substances. This

group could possibly be extended to include *M. anterior*, and there are probably some affinities to species of Groups H and I.

H. *M. contexta – M. eximia – M. nigella – M. olivacea*
Th. endoxylic, or forming a thin crust, or weakly areolate. Pigments A and (or) B in various locations. Spores simple or 1-septate. Paraphyses dimorphic. Pyc. black, immersed to sessile, or stalked (*M. nigella*). Macroconidia unknown. Chemistry: no substances. Mainly lignicolous and confined (?) to north-west Europe. Probably close to Group G. *M. melaena* may belong here but has: rather large apothecia, pigment C (usually present in hypothecium), an often well-developed, areolate thallus containing gyrophoric acid, and an ability to produce macroconidia; it may provide a link between Group H and Groups A–D.

I. *M. bauschiana – M. sylvicola – M. tuberculata – M. lutulata*
Th. weakly areolate, ± smooth or scurfy. Phycobiont non-micareoid. Pigmentation variable, involving pigments A, B, C, and F; pigment D never present. Spores small, simple, or *p.p.* 1-septate (*M. tuberculata*). Paraphyses dimorphic. Pyc. ± immersed. Macroconidia unknown. Chemistry: no substances. Mainly found in dry underhangs in the *Micareetum sylvicolae.* This group is almost worthy of subgeneric status but it shows some affinities to Group G, and other species, such as *M. lithinella*.

J. *M. assimilata – M. incrassata – M. subviolascens – M. melaenida – M. crassipes*
Th. areolate-type, sometimes with AL. Pigmentation variable, involving pigments A, B, C, D, and E; Hyp. always dark-coloured. Spores rather large, mostly ellipsoid or oblong-ellipsoid and simple or 1-septate. Paraphyses rather stout and sparingly branched. Cephalodia found in first three species. Pyc. immersed. Macroconidia unknown. Chemistry: no substances. Mainly terricolous or muscicolous (never corticolous or lignicolous), and with a ± arctic or arctic-alpine distribution (except *M. melaenida*). *M. crassipes* is rather anomalous here because of its very well-developed excipulum and turbinate or stipitate apothecia.

K. *M. prasina – M. hedlundii – 'Lecidea' levicula* [from Cuba]
Th. goniocyst-type. Hym., Pyc. and Th. often with pigment D; Hyp. hyaline; one species (*M. hedlundii*) with pigment H. Spores mostly simple or 1-septate. Pyc. immersed to sessile, or stalked and tomentose (*M. hedlundii*). Micro- and (or) mesoconidia produced; macroconidia unknown. Chemistry: variable, including 'prasina unknowns' and gyrophoric acid. *M. misella* and *M. melanobola* have some affinities to this group, but also with Group D. *M. synotheoides* may belong near here.

Keys to species

Guide to keys and identifications

Two keys are provided, the first to specimens with apothecia, the second to specimens without apothecia (although often with pycnidia). The keys are for European species, but all those known to me from cool-temperate, boreal, and arctic regions of North America are, by chance, included.

The nature of pigmentation and colour reactions observed in anatomical sections is important for the identification of *Micarea* species. Many of the subtle yet significant colour hues and reactions are obscured by the yellowish illumination given by most bulbs, and it is recommended that a microscope be fitted with a 'daylight' bulb or a blue filter. The preceding sections on 'Morphology' and 'Chemistry' should be read *before* attempting to use the keys.

Particular care should be taken in determining C reactions with apothecial sections. The straw to dull olivaceous, K+ violet pigment found, for example, in *M. prasina, M. synotheoides, M. denigrata,* and *M. nitschkeana,* also reacts C+ violet (persistent); this reaction tends to mask the C+ orange-red (quickly fading) reaction due to gyrophoric acid and usually obtainable in the last two, aforementioned species. However, the C+ violet reaction is mostly confined to the upper part of the hymenium, whereas the C+ orange-red reaction occurs in all parts of the apothecium. To carry out the C test cut a hand section of an apothecium and mount in a drop of water near the edge of the cover-slip; lay a piece of tissue-paper over the cover slip to take up any excess water; place the slide preparation on the microscope stage and focus at about ×100 to ×200 and note any pigmentation; then, apply a drop of C by the edge of the cover-slip nearest the section. A positive reaction due to gyrophoric acid is seen as an orange-red front moving across the section, with the colour quickly fading in its wake. If the concentration of gyrophoric acid is very high than the reaction may be more immediate and intense, but, nevertheless, the colour quickly fades away within a few seconds. A similar procedure should be followed when testing for other colour changes.

The identification of *Micarea* species usually requires accurate measurement of the dimensions of spores, conidia, and paraphyses, such that a microscope with a good resolution at ×1000, coupled with a carefully calibrated measuring eyepiece, is invaluable, and in many cases essential.

Spores should be observed and measured in 10% KOH; in most cases this solution will render any septa visible. If, however, the spore contents are difficult to clear, septa can be discerned by preparing an apothecial section or squash in LCB and heating (*just* to boiling) over a spirit lamp; any septa should then be clearly seen, especially under oil-immersion (×1000).

Conidia should always be examined under oil-immersion (at least ×1000). Preparations can be made in 10% KOH, but better resolution is obtained using ammoniacal erythrosin. In water, small conidia are prone to 'Brownian movement', making alignment with the measuring graticule a frustrating task! If conidia and conidiogenous cells are to be examined in a squash preparation it is often helpful to soak an intact pycnidium in a small drop of 10% KOH on a slide for about a minute; excess KOH is then soaked up with the edge of a piece of tissue-paper or filter-paper and the squash prepared under a cover-slip in ammoniacal erythrosin. The KOH softens the pycnidial wall and does not alter the effectiveness of the erythrosin.

Fine measurements, such as the width of spores, conidia, hyphae, and paraphyses should not be made in LCB, this solution often causing much shrinkage; with hyphae and paraphyses the cytoplasm (lumina) is intensely stained, but the delimitation of their outer walls is often difficult to ascertain.

Key to European species

1a Hymenium, at least in upper part, dull greenish or brownish in water, K+ violet [pigment D].. 2
1b Hymenium variously coloured or hyaline, not turning to violet in K (if purple in K, then pigment already purplish in water [pigment C] 12

2a (1a) Hypothecium dark purple-brown, K+ purple intensifying or K+ green in upper part. Saxicolous........ **40. M. subviolascens** (p. 185)
2b Hypothecium hyaline or pale. Usually corticolous or lignicolous 3

3a (2b) Spores mostly 3 (or more)-septate, or over 15 μm long 4
3b Spores mostly simple or 1-septate (2- or 3-septate spores if present very rare), mostly less than 15 μm long 8

4a (3a) Apothecia sections and/or thallus C+ orange-red (gyrophoric acid) 5
4b Apothecia sections and thallus C− [note: the K+ violet pigment also reacts C+ violet], gyrophoric acid absent 7

5a (4a) Spores 0–1(–2)-septate, few exceeding 16 μm in length. Usually lignicolous. Rare forms of this very variable species .... **11. M. denigrata** (p. 127)
5b Spores mostly 3 (or more)-septate, or many exceeding 16 μm in length. Usually on bark or twigs........ 6

6a (5b) Spores (1–)3-septate, fusiform, often curved, 10–17(–19)×2·5–3(–3·5) μm. Microconidia (4·7–)5·5–7·5×0·8 μm; mesoconidia (3–)3·5–5(–5·7)×1–1·5 μm; macroconidia sometimes present, curved........ **30. M. nitschkeana** (p. 165)
6b Spores 0–3(–6)-septate, acicular, 13–26×1·5–2·5(–3) μm. Microconidia 3·8–5×0·8–1 μm; mesoconidia 3·6–5·3×1–1·4 μm; macroconidia unknown .... **14. M. globulosella** (p. 134)

7a (4b) Thallus dull grey-green (never whitish) to dark olivaceous or blackish, of discrete or coalescing granular-areolae *c.* 20–70 µm diam, ± gelatinous when wet. Phycobiont micareoid, cells 4–8 µm diam. Apothecia grey- or brown-black, epruinose. Spores 1–5(–11)-septate, 14–35(–43)×1·8–2·5(–3) µm. Microconidia and/or mesoconidia often present, both exceeding 3·7 µm in length. An oceanic species on acid bark (sometimes over bryophytes) .... **42. M. synotheoides** (p. 188)

7b Thallus whitish, tinged grey or green, ± endophloeodal or thin and smooth to ± verrucose, often rimose; never gelatinous. Phycobiont not micareoid, cells 8–16 µm diam. Apothecia grey to black, often with whitish pruina. Spores (1–)3–7-septate, 17–26×1·5–2·5 µm, Excipulum hyphae coherent in K. Conidia of one type only, 2·8–3·5×1–1·4 µm. Widespread species on rather basic bark, rarely on lignum .... **Bacidia beckhausii**

8a (3b, 31a) Thallus of pale to dark green goniocysts *c.* 12–40(–60) µm diam, often ± gelatinous when wet, C−, gyrophoric acid absent or detectable in trace amounts (?contaminant) by t.l.c. 9

8b Thallus endoxylic or of whitish or grey granular-areolae *c.* 60–200 µm diam, not appearing gelatinous when wet, C or C+ orange-red, gyrophoric acid often present 11

9a (8a) Goniocysts K− or hyphae violaceous in K, pigment never oily. Pycnidia immersed or sessile, not tomentose 10

9b Goniocysts containing purple oily substance in K. Pycnidia numerous, distinctly stalked, brown with white tomentum; containing mesoconidia (4–)4·5–5·5(–6)×1·3–1·7 µm. Apothecia usually few or absent, brown, soon tuberculate. On soft lignum of conifers, rare .... **15. M. hedlundii** (p. 135)

10a (9b) Apothecia dark grey to black, small, 0·1–0·24 mm diam. Paraphyses with dark apical walls giving a distinct dark green, K+ violet epithecium. Spores 0–1-septate, 7–9·7×2·5–3·3 µm. Microconidia 4–5·5×0·7–0·8 µm; mesoconidia 3·3–4·5×1–1·3 µm. Thallus indistinct, of scattered olivaceous goniocysts. Rare, (?) confined to *Picea* bark in S. Finland .... **25. M. melanobola** (p. 156)

10b Apothecia white to grey, sometimes blackish, 0·1–0·4 mm diam. Without sharply delimited epithecium, the olivaceous, K+ violet pigment mostly confined to the gel-matrix and ± diffuse although often more concentrated towards upper part of hymenium. Spores variable, 0–1(–3)-septate, 8–14(–17)×2·3–4(–5) µm. Microconidia (5–)5·5–8×0·7–1 µm; mesoconidia 3·5–4·7×1·4–1·8 µm. Thallus of thinly scattered to coherent goniocysts, sometimes forming a thick crust. Common and widespread on bark, lignum and turf (especially coastal), rare on rock; morphologically and chemically very variable .... **34. M. prasina** (p. 173)

11a (8b) Apothecia grey to black, sometimes pallid or brown (shade forms), 0·1–0·5 mm diam. Thallus of distinct whitish areolae, or dark and scurfy (parasitized), occasionally endoxylic. Spores mostly 1-septate, often ± curved, (7–)9–16(–18)×2–3·3(–3·5) µm. Paraphyses numerous, *c.* 1–1·5 µm wide. Pycnidia immersed or emergent, never distinctly stalked. Microconidia (4·5–)5–7·5×0·7–0·8 µm; mesoconidia 2·8–4·5(–5)×1·2–1·8 µm; macroconidia curved, 12–24×1 µm. Apothecia and thallus sections usually C+ orange-red (gyrophoric acid) .... **11. M. denigrata** (p. 127)

11b Apothecia black (very rarely paler), smaller, 0·1–0·3 mm diam. Thallus usually endoxylic, rarely forming whitish areolae. Spores mostly simple, 1-septate spores rarely numerous, never curved, 6·5–9·5×2–3(3·7) µm. Paraphyses scanty, thin, 0·5–0·8 µm wide. Endoxylic forms usually with black, stalked pycnidia containing mesoconidia, 3·5–5×1–1·5 µm; microconidia 3·8–6×0·7–0·8 µm, borne in immersed pycnidia; macroconidia unknown. Apothecia sections usually C−, very rarely C+ orange-red; thallus when superficial and well developed C+ orange-red (gyrophoric acid) .... **26. M. misella** (p. 158)

12a (1b) Spores acicular or sigmoid-curved (mostly over 18 µm long *and* under 3·5 µm wide at maturity) 13

12b Spores not acicular or sigmoid-curved 15

13a (12a) Apothecia whitish, without pigmentation, epruinose, C+ red or C−. Phycobiont micareoid, cells 4–7 µm diam. Pycnidia always abundant, sessile or stalked, whitish 14

13b Apothecia dark coloured (with brownish or greenish pigment in upper hymenium); if whitish then pruinose (epithecium finely granular) or not. Phycobiont not micareoid, many cells over 8 µm diam. Pycnidia (?) unknown; if present, then never conspicuous or stalked .... **Scoliciosporum** species [see Poelt & Vězda (1981)]

14a (13a) Apothecia and pycnidia C+ red (gyrophoric acid). Pycnidial structures mostly unbranched, 0·1–0·3 mm tall; containing mesoconidia 4–6 × 1–1·5 µm .... **35. M. pycnidiophora** (p. 179)
[if spores fusiform and pycnidia immersed, see 23]

14b Apothecia and pycnidia C−. Pycnidial structures often branched, 0·3–0·8 mm tall; containing mesoconidia 6–8 × 1–1·8 µm .... **37. M. stipitata** (p. 182)

15a (12b) Mature spores 3- or more septate, mostly over 15 µm long 16

15b Mature spores simple or 1-septate 28

16a (15a) Upper hymenium with distinct epithecial layer of dense fuscous-brown pigment (without green or purple tinge), K+ dissolving into a brown solution. Spors 0–1(−3)-septate, (9–)11–15(–20) × 2–3·5 µm. Hypothecium pale. Usually lignicolous .... **12. M. elachista** (p. 131)

16b Upper hymenium otherwise, if brownish then pigment not dissolving into a brown solution. Hypothecium hyaline, pale or dark. Substrata various 17

17a (16b) Upper hymenium purple, K+ intensifying. Hypothecium dark purple-brown. Rare form of .... **22. M. melaena** (p. 150)

17b Upper hymenium hyaline, greenish (sometimes tinged brown) or aeruginose 18

18a (17b) Hypothecium dark in thin section 19

18b Hypothecium hyaline or with dilute greenish or brownish tinge 20

19a (18a) Hypothecium mottled reddish brown, K−, HNO_3− or + orange-brown. Upper hymenium greenish, sometimes brownish in part. Hyaline paraphyses 1–1·5 µm wide. Thallus always C− (gyrophoric acid absent); terricolous .... **45. M. turfosa** (p. 194)

19b Hypothecium dark purplish brown, K+ green or K+ purple intensifying (often a mixture of both reactions, HNO_3+ purple-red. Hyaline paraphyses 0·8–1 µm wide. Thallus when well developed C+ red (gyrophoric acid) .... **22. M. melaena** (p. 150)

20a (18b) Apothecia whitish, without pigmentation, C+ red (gyrophoric acid). Spores mostly 3-septate 21

20b Apothecia pale grey to black, often with a greenish tinge; if whitish then spores mostly 7-septate (*M. cinerea*). Upper hymenium greenish to aeruginose. Apothecia sections C−, or C+ orange-red (gyrophoric acid). Spores 3- or more septate 22

21a (20a) Apothecia usually numerous and crowded. Spores 3(–5)-septate, (16–)17–26(–28) × 4–5(–6) µm. On bark and lignum, often over bryophytes, in oceanic areas .... **2. M. alabastrites** (p. 110)

21b Apothecia usually dispersed and usually with some hint of pigmentation. Spores (1–)3(–5)-septate, (11–)15–23(–24) × 3–5(–6) µm. Shade forms, occurring on bark of old trees (especially *Quercus*) or on rocks, of this widespread and variable species of various substrata (see 27a) .... **33. M. peliocarpa** (p. 169)

22a (20b) Thallus of fragile (easily broken with point of dissecting needle), ash-grey to grey-brown granular-areolae, often dissolving to form sorediate patches, PD+ yellow or red. Usually sterile 23

22b Thallus of firm areolae or granules, or endoxylic, PD− or PD+ red (*M. lignaria*). Apothecia usually numerous 24

23a (22a) Thallus C+ red, PD+ red (gyrophoric acid and argopsin). Spores (1–)3-septate, 14–26(–29) × 4–5·5 µm .... **18. M. leprosula** (p. 140)

23b Thallus Cf+ red, KC+ red, PD+ deep yellow (alectorialic acid). Spores 3–7(–9)-septate, 35–45(–60) × 5–6·5 µm .... **38. M. subleprosula** (p. 182)

24a (22b) Thallus PD+ red and C− (argopsin), or PD− and C+ persistent orange (xanthone); gyrophoric acid absent. Apothecia black, ± globose, sessile or occasionally stipitate. Upper hymenium green (sometimes brownish in reflexed parts). Hypothecium pale, dilute greenish or brownish in upper part. Spores 3–7-septate, 16–36(–38)×4–6(–7) μm.............. 25

24b Thallus PD−; thallus and/or apothecia sections C+ red (soon fading; gyrophoric acid) or C− (no substances). Apothecia often adnate at first 26

25a (24a) Areolae C−, PD+ red (argopsin), usually whitish or pale grey. Widespread and common, especially in upland areas.............. **19a. M. lignaria** var. **lignaria** (p. 142)

25b Areolae C+ persistent orange, PD− (xanthone), usually whitish with yellowish (isabelline) tinge. Local, confined to high rainfall areas, often with var. *lignaria*.............. **19b. M. lignaria** var. **endoleuca** (p. 146)

26a (24b) Spores (3–)5–7-septate, (19–)23–34(–34(–38)×4·5–6 μm. Macroconidia filiform, flexuose, 50–110×1 μm. Thallus and apothecia sections C+ red (gyrophoric acid) .... **7. M. cinerea** (p. 121)

26b Spores mostly 3-septate (5–septate spores absent or in very low frequency), less than 25 μm long. Macroconidia less than 50 μm long. Thallus and apothecia sections C+ red or C− 27

27a (26b) Thallus and apothecia sections C+ red (gyrophoric acid). Hypothecium usually hyaline. Microconidia (5–)6–7(–7·7)×0·4–0·7 μm; mesoconidia unknown; macroconidia curved, 21–40(–47)×1–1·5 μm. Widespread on various substrata .... **33. M. peliocarpa** (p. 169)

27b Thallus and apothecia sections C− (no substances with t.l.c.). Hypothecium with green-brown tinge (as in *M. lignaria*). Microconidia and macroconidia unknown; mesoconidia 4·6–6·3–1·2–1·7 μm. On turf in the Arctic; possibly occurring in western Britain on rocks in coastal districts as a form with a ± obsolete thallus .... **43. M. ternaria** (p. 190)

28a (15b) Thallus of well developed, whitish to grey-brown, convex granular-areolae, 0·08–0·4 mm diam, with intermixed brown cephalodia containing *Nostoc* or *Stigonema*. Apothecia black, convex to subglobose, never markedly constricted below. Spores simple, or 1(–2)-septate spores intermixed, 10–17(–19)×3–5 μm. Upper hymenium green, K−. Hypothecium dark. Over bryophytes, plant debris or light soil amongst rocks or on exposed turf in montane or Arctic regions 29

28b Without the above combination of characters; never with cephalodia 30

29a (28a) Hypothecium reddish brown, K−, HNO_3+ bright orange-brown (no purplish tinge). Thallus usually grey-brown. Spores simple or often 1-septate (rarely 2-septate) .... **16. M. incrassata** (p. 137)

29b Hypothecium purple-brown, K+ purple intensifying, HNO_3+ purple-red. Thallus usually whitish or brownish white. Spores mostly simple, septate spores very rare .... **4. M. assimilata** (p. 114)

[if young apothecia turbinate and thallus finely granular, see 51b]

30a (28b) Apothecia whitish, pallid or dull reddish, without distinct pigmentation in section. Spores mostly 1-septate and over 9 μm long. Phycobiont micareoid. On bark or lignum or over bryophytes thereon.............. 31

30b Apothecia coloured with obvious pigmentation in section; if not then, spores simple and/or smaller, *or* on rock, *or* phycobiont not micareoid 33

31a (30a) Thallus comprised of goniocysts/or apothecia sections C+ red (gyrophoric acid) and spores less than 3 μm wide. Shade forms 8

31b Thallus not comprised of goniocysts, endoxylic or weakly areolate, or scurfy granular, or rimose, sometimes with waxy appearance. All parts C− (gyrophoric acid absent). Spores often over 3 μm wide 32

32a (31b) Apothecia pale reddish or orange-brown, small, 0·15–0·35 mm diam, sometimes tuberculate and up to 0·6 mm diam, but never forming large nodulose clusters. Spores ovoid-fusiform, often slightly curved, (0–)1(–3)-septate, 9–16×2·5–4·5 μm. Pale reddish brown, stalked pycnidia often present. Thallus usually poorly developed, never waxy .... **3. M. anterior** (p. 112)

32b Apothecia pallid, at first ± plane and adnate, 0·2–0·4(–0·6) mm diam, later often coalescing to form large nodulose clusters up to 2 mm wide. Spores ellipsoid, ovoid or oblong, never curved, (0–)1-septate, 9–16×3–5 μm. Without stalked pycnidia, but white, convex sporodochia (0·1–0·25 mm diam) usually present, bearing simple, ellipsoid macroconidia, 6–10×2–3 μm .... **1. M. adnata** (p. 108)

33a (30b) Thallus and apothecia sections C+ red (? gyrophoric acid). Epithecium fuscous-brown. Hypothecium pale. Spores markedly curved, 1-septate, 9–12×2·5–4 μm. On rock .... **10. M. curvata** (p. 126)

33b Thallus and apothecia sections C−; without remaining combination of characters 34

34a (33b) Upper hymenium with well defined fuscous-brown epithecium, pigment unchanged in colour but dissolving into solutions in K. Hypothecium hyaline to dilute yellowish brown. Phycobiont micareoid. Mostly on lignum or old bark 35

34b Upper hymenium otherwise; if fuscous-brown then pigment not dissolving in K and plant not on bark or lignum. Hypothecium hyaline, pale or dark. Phycobiont micareoid or not. Substrata various 36

35a (34a) Spores 0–1(–3)-septate, (9–)11–15(–19)×2–3·5 μm. Thallus of dispersed to contiguous, whitish, grey-brown or olivaceous-brown, convex to ± globose areolae. On lignum or old bark, very rarely on rock .... **12. M. elachista** (p. 131)

35b Spores 0(–1)-septate, 6–9·5×1·5–2·3 μm. Thallus endoxylic. On lignum .... **36. M. rhabdogena** (p. 181)

36a (34b) Hypothecium hyaline, yellowish, dilute orange-brown or dilute greenish, not blackish in thick sections 37

36b Hypothecium dark throughout, often blackish in thick section 42

37a (36a) Apothecia dark brown or black. Spores 0–1-septate, *c.* 9–14×4–6 ± m. On exposed rocks 38

37b Apothecia pale; if dark then spores simple and/or smaller. In sheltered situations on shaded rocks, exposed tree-roots etc 39

38a (37a) Upper hymenium brown. Phycobiont micareoid. Pycnidia usually present, with either helicoid macroconidia or cylindrical microconidia .... **39. M. subnigrata** (p. 183)

38b Upper hymenium green. Phycobiont not micareoid, thick-walled, 7–21 μm diam. Pycnidia unknown .... **17. M. intrusa** (p. 138)

39a (37b) Spores small, in range, 4–8·5×1–2·5 μm, single or 1-septate. Apothecia small, mostly less than 0·3 mm diam 40

39b Spores larger, *c.* 7–10×3–4·5 μm, simple. Apothecia usually larger, often more than 0·3 mm diam 41

40a (39a) Spores mostly 1-septate, 6–8·5×1·5–2·5 μm. Apothecia orange-brown or reddish brown. Hypothecium dilute orange-brown. Phycobiont (?) micareoid, cells 4–7 μm .... **28. M. myriocarpa** (p. 161)

40b Spores simple, 3–6×1–2 μm. Apothecia blue-grey to blackish. Hypothecium dilute green. Phycobiont cells 5–12(–18)×3–8 μm, often in pairs or short chains **Psilolechia clavulifera** (p. 201)

41a (39b) Phycobiont not micareoid, cells 5–12 μm diam. Apothecia pallid to black. Upper hymenium hyaline to dark green or aeruginose. Hypothecium hyaline, or dilute greenish in upper parts .... **5. M. bauschiana** (p. 117)

41b Phycobiont micareoid, cells 4–8 μm diam. Apothecia pallid, dull yellowish-orange to reddish brown. Upper hymenium hyaline. Hypothecium straw-yellow to dilute orange-brown .... **20. M. lithinella** (p. 147)

42a (36b) Hypothecium fuscous or ± reddish brown, without distinct purple or greenish tinges in water or K, HNO_3− or + bright orange-brown, never + purple-red 43

42b Hypothecium with distinct purple or greenish tinge in water and/or K, HNO_3+ purple-red 50

43a (42a) Pycnidia conspicuous, black, sessile or stalked 44

43b Pycnidia inconspicuous and immersed, or absent 45

44a (43a) Spores simple, 5–9×2·5–3·8 μm. Conidia 2·6–3·6×1–1·3 μm. On lignum .... **24. M. melaeniza** (p. 155)

44b Spores 0–1(–3)-septate, 8–13(–16)×2.3–4 μm. Conidia 3·5–4·8×1–1·5 μm. On shaded rocks, decaying bryophytes, exposed tree roots or loose stones, rarely on bark or lignum .... **6. M. botryoides** (p. 118)

45a (43b) On rocks, loose stones, consolidated soil, dry bryophyte mats or exposed tree roots in underhangs, *or* on lignum 46

45b On mineral soil, or over decaying bryophytes or plant debris on the ground; never in underhangs 48

46a (45a) Spores mostly 1-septate, 6–8·5×1·5–2·5 μm. Hymenium hyaline or tinged orange-brown, never greenish. Hypothecium never blackish .... **28. M. myriocarpa** (p. 161)

46b Spores simple. Hymenium often greenish or ± aeruginose. Hypothecium blackish in thick section 47

47a (46b) On sheltered rocks, rarely on exposed tree roots. Apothecia convex-globose, often tuberculate. Spores 6–8(–9)×2–3(–3·4) μm. Hypothecium *c.* 120–360 μm tall. Phycobiont not micareoid, cells 5–12 μm diam .... **21. M. lutulata** (p. 148)

47b On lignum, rarely on rock. Apothecia convex-adnate, never tuberculate. Spores 9–12×4–5 μm. Hypothecium *c.* 70–120 μm tall. Phycobiont micareoid, cells 4–7 μm diam .... **27. M. muhrii** (p. 160)

48a (45b) Spores simple, small, 6–9·5×3–4 μm. Upper hymenium brown without green or purple tinge in K. On exposed soil in woodland clearings (? sites of old bonfires) .... **32. M. osloensis** (p. 169)

48b Spores larger, mostly over 10 μm long. Upper hymenium usually with greenish or purple tinge in K 49

49a (48b) Thallus blackish. Upper hymenium usually with green tinge in K. Spores simple, or often becoming 3-septate (10–)12–21(–25)×(3·5–)4–5 μm. On exposed soil or truf on mountain summits or exposed ridges, or at lower altitudes in boreal regions **45. M. turfosa** (p. 194)

49b Thallus whitish. Upper hymenium with purple tinge in K. Spores 0–1-septate, (7–)9·5–15×3–4(–4·5) μm. On fine-sandy or argillaceous soil .... **23. M. melaenida** (p. 154)

50a (42b) Thallus terricolous or muscicolous. Spores simple or 1-septate, mostly in range 9–19×3–4·5 μm. Paraphyses numerous, simple or sparingly branched, 1–1·5 μm wide 51

50b Thallus saxicolous, lignicolous or corticolous, not terricolous or if so (anomalous occurrences) then spores smaller *or* paraphyses thinner and much branched 52

51a (50a) On fine sandy or argillaceous soils, never muscicolous or on plant debris; at low altitudes. Apothecia immarginate, convex to hemisphaerical, adnate when young; in section without greenish pigmentation in K. Spores 1-septate, (7–)9·5–15×3–4 μm .... **23. M. melaenida** (p. 154)

51b On bryophytes or plant debris, sometimes spreading on to sandy soil; in Arctic or Alpine situations. Apothecia, at least when young, marginate, and markedly constricted below, turbinate or short-stalked; in section (especially excipulum) with green pigmentation (often mixed with purple pigmentation) in K. Spores mostly simple, (9–)10–19(–21)×(2·5–)3–4·5 μm .... **9. M. crassipes** (p. 125)

52a (50b) Phycobiont not micareoid, cells 5–12 μm or more in diam. On shaded rocks in humid places (narrow ravines or woodlands), or in sheltered underhangs on rock, loose stones, exposed roots or consolidated soil; rarely on lignum (old fence posts) 53

52b Phycobiont micareoid, cells 4–8 μm diam. Usually on lignum, rarely on shaded rock 56

53a (52a) Hypothecium dark reddish brown, K− or K± red intensifying, but not turning purplish or greenish. Hymenium hyaline, dilute green to aeruginose. Spores 6–8(–9)×2–3(–3·4) μm .... **21. M. lutulata** (p. 148)

53b Hypothecium distinctly greenish in K, more rarely purplish in part or in whole 54

54a (53b) Spores ellipsoid or ovoid-ellipsoid, (6–)7–10×(2·3–)3–4·5 µm. Apothecia 0·2–0·5 mm diam, or reaching 1·2 mm when tuberculate. Conidia 3·8–6(–6·6)×1–1·7(–2) µm .... **41. M. sylvicola** (p. 186)
54b Spores ovoid, oblong-ovoid or dacryoid, never ellipsoid, smaller, mostly less than 8 µm long and 2·4 µm wide. Non-tuberculate apothecia usually smaller, rarely exceeding 0·3 mm diam. Conidia, if present, shorter 55

55a (54b) Spores 0–1-septate, 5–8(–9)×1·5–2·5 µm. Hypothecium much darker than hymenium. Pycnidia often present, 60–120 µm diam; wall dark green. Conidia 3–4·3×1–1·4 µm. Phycobiont cells ± globose, *c.* 5–12 µm diam, never in short chains .. **44. M. tuberculata** (p. 192)
[if similar but phycobiont micareoid, see 58a]
55b Spores simple, 3–6×1–1·7(–2) µm. Hypothecium concolorous with, or paler than, hymenium. Pycnidia unknown. Phycobiont cells ± globose, ellipsoid or oblong, 5–12(–18)× 3–8 µm, often in pairs or short chains .... **Psilolechia clavulifera** (p. 201)

56a (52b) Spores simple, 6·5–10×2·5–3·7 µm. Sessile or stalked, black pycnidia present. Hypothecium purple-brown, K+ green.............. **29. M. nigella** (p. 163)
56b Spores (0–)1-septate. Pycnidia innate, never stalked 57

57a (56b) Spores narrow, oblong-fusiform, 9–14(–16)×1·8–2·5 µm. Hypothecium purple-brown, K+ green. Hymenium bright green in upper part. Hyaline paraphyses rather scanty, thin, 0·7–0·8 µm wide. Pycnidia with mesoconidia 3·9–5·5×1–1·4 µm .... **13. M. exima** (p. 134)
57b Spores broader, 2·5 µm or more in width, oblong with ± rounded apices, or ovoid 58

58a (57b) Hyaline paraphyses numerous, 1–1·2 µm wide. Hypothecium dark sordid-olivaceous or olive-brown, without any purple tinge in water or K. Hymenium olivaceous green. Spores oblong or ovoid-oblong, (0–)1-septate, (7–)9–12·3×2·5–3·5 µm. Pycnidia with mesoconidia 3–4·2×1–1·3 µm .... **31. M. olivacea** (p. 167)
58b Hyaline paraphyses scanty or numerous, thin, 0·6–1 µm wide. Hypothecium often with purple tinge in water or K, green and purple pigments often intermixed.............. 59

59a (58b) Spores ovoid or oblong ovoid, 1-septate, 7–13(–14)×(2·3–)3–4·5 µm. Apothecia 0·1–0·2 µm diam, or reaching 0·3 mm when tuberculate. Thallus endoxylic. Microconidia 4–5×0·8–1 µm; mesoconidia 3·8–4·7×1·3–1·8 µm; macroconidia unknown.............. **8. M. contexta** (p. 124)
59b Spores oblong or ovoid oblong, at first 1-septate, becoming 3-septate at maturity. Apothecia 0·12–0·4 mm diam, or reaching 0·5 mm when tuberculate. Thallus superficial, containing gyrophoric acid when well developed. Microconidia 4·8–7×0·8–1 µm; mesoconidia unknown; macroconidia curved, 18–33×1–1·5 µm. Immature forms .... **22. M. melaena** (p. 150)

Key to European species that may occur without apothecia

Notes: all species included here have micareoid algae; all species with stalked pycnidia are included here.

1a Thallus of fragile ash-grey or grey-brown granular-areolae often dissolving or eroding to form sorediate patches; PD+ yellow or red. Pycnidia absent 2
1b Thallus otherwise, PD–. Pycnidia usually present and conspicuous (×20 lens) 3

2a (1a) Thallus C+ red, PD+ red (gyrophoric acid and argopsin) .... **18. M. leprosula** (p. 140)
2b Thallus C+ red (often faint), KC+ red, PD+ deep yellow (alectorialic acid) .... **38. M. subleprosula** (p. 182)

3a (1b) With stalked or sessile pycnidia containing mesoconidia (smaller ± immersed pycnidia containing microconidia sometimes present); never with curved or flexuose macroconidia 4
3b Pycnidia innate sometimes becoming emergent with gaping ostioles, *or* with small sessile apothecia-like sporodochia; pycnidia sometimes containing curved or flexuose macroconidia 11

4a (3a) Pycnidia black.............. 5
4b Pycnidia whitish to reddish brown, never black 8

5a (4a) Pycnidial wall olivaceous brown, K+ violet. Mesoconidia 3·5–5×1–1·5(–1·7) µm .... **26. M. misella** (p. 158)
5b Pycnidial wall K– or K+ olivaceous 6

6a (5b) Pycnidial wall and stalk dark purple-brown, K+ dark green. Mesoconidia 3·4–4·3×1·2–1·6 μm .... **29. M. nigella** (p. 163)

6b Pycnidial wall dark olivaceous, K−; stalk fuscous or reddish-brown, K− 7

7a (6b) Mesoconidia 3·5–4·8×1–1·5 μm. On bryophytes, shaded rocks and stones or exposed roots, rarely on lignum .... **6. M. botryoides** (p. 118)

7b Mesoconidia 2·6–3·6×1–1·3 μm. On lignum .... **24. M. melaeniza** (p. 155)

8a (4b) Thallus of pale to dark green goniocysts, 12–40 μm diam; goniocysts containing purple oily substance in K. Pycnidia brown with white tomentum. Mesoconidia (4–)4·5(–6)×1·3–1·7 μm .... **15. M. hedlundii** (p. 135)

8b Thallus indistinctly areolate or rimose, or endoxylic, without goniocysts, K−. Pycnidia without tomentum 9

9a (8b) Pycnidia whitish, C+ red (gyrophoric acid). Mesoconidia 4–6×1–1·5 μm .... **35. M. pycnidiophora** (p. 179)

9b Pycnidia C−, whitish or reddish brown 10

10a (9b) Pycnidia whitish, often branched. Mesoconidia 6–8×1–1·8 μm. Usually on bark, in oceanic areas .... **37. M. stipitata** (p. 182)

10b Pycnidia reddish brown, rarely branched. Mesoconidia 3·5–4·5×1·2–1·6 μm. On lignum in boreal regions .... **3. M. anterior** (p. 112)

11a (3b) With whitish, cushion-like, apothecia-like sporodochia *c.* 0·1–0·25 mm diam, bearing oblong-ellipsoid macroconidia 6–10×2–3 μm (immersed, inconspicuous pycnidia containing mesoconidia 4–5·3×1·2–1·5 μm may also be present). All parts C− (t.l.c.: nil). On lignum or decaying bark of old stumps .... **1. M. adnata** (p. 108)

11b Sporodochia absent. Thallus and/or pycnidia C+ red (gyrophoric acid) or C− (t.l.c.: 'prasina unknowns') 12

12a (11b) Thallus of pale to dark green (sometimes K+ violet) goniocysts 12–60 μm; pycnidia, if present, 30–80 μm diam containing either (5–)5·5–8×0·7–1 μm microconidia, or (3·5–)4–6×1·2–1·7 μm mesoconidia. All parts C− (t.l.c.: 'prasina unknowns') .... **34. M. prasina** (p. 173)

12b Thallus areolate, or scurfy (invaded by dematiaceous hyphae and foreign algae), or ± endoxylic; thallus and/or pycnidia usually C+ red (gyrophoric acid); sometimes with curved or flexuose macroconidia 13

13a (12b) With numerous pycnidia containing mesoconidia, 3·5–4·5×1·3–2 μm, often extruded as conspicuous white blobs; in addition, pycnidia containing microconidia (4–)4·5–6(–6·5)×0·7–1 μm, or curved macroconidia 12–12×1 μm, sometimes present; pycnidia walls with pale olivaceous pigment, K+ violet. Usually on lignum, commonly on worked timber .... **11. M. denigrata** (p. 127)

13b Pycnidia usually with longer, curved or flexuose macroconidia; smaller pycnidia with microconidia sometimes present; mesoconidia unknown; pycnidial walls hyaline or greenish, K−. On various substrata, rarely on worked timber 14

14a (13b) Macroconidia curved or hamate, 21–40×1–1·5 μm. Microconidia (5–)6–7(–7·7)×0·4–0·7 μ,. On various substrata but most commonly encountered without apothecia on bark of old trees (especially *Quercus*) in old woodlands .... **33. M. peliocarpa** (p. 169)

14b Macroconidia flexuose, 50–110×1 μm. Microconidia (3·8–)4–5×0·5–0·7 μm. Seen without apothecia on shaded lignum in woodland, and over bryophytes in open montane situations .... **7. M. cinerea** (p. 121)

The species

1. **Micarea adnata** Coppins, **sp. nov.**
(Figs 7A, 36–37; Map 1)

Thallus effusus, tenuis, ± laevis vel furfuraceo–granulosus, pallide griseo-viridis, plerumque nonnihil cereus. *Algae* cellulis 4–7 μm diam. *Apothecia* pallide eburnea vel straminea vel demum pallide rufescentia, immarginata, adnata, primum planiuscula mox convexa, 0·2–0·4(–0·6) mm diam, interdum coalescentia in fasciculosos noduliformes ad 2 mm diam. *Hymenium* 35–40 μm altum, ± hyalinum. *Ascosporae* ellipsoideae, ovoideae, oblongo-ellipsoideae, oblongo-ovoideae vel oblongae, (0–)1-septatae, 9–16×

3–5 μm. *Paraphyses* numerosae, ramosae et anastomosantes, *c.* 1–1·5 μm latae, apicibus vix incrassatis. *Hypothecium* hyalinum. *Excipulum* bene evolutum et manifestum praesertim in apotheciis junioribus. *Conidiomata* pycnidiiformia et sporodochiiformia. *Pycnidia* pauca et inconspicua, ± immersa, alba, *c.* 40–60 μm diam, producentia conidiis cylindricis 4–5·3×1·2–1·5 μm. *Sporodochia* plerumque numerosa et conspicua, alba, pulvinata, 20–250 μm diam, producentia conidiis cylindricis vel oblongo-ellipsoideis 6·5–9·5×2·3–3 μm. *Thallus* et *apothecia*, K–, C–, PD–; sine materia chemica.

Typus: Caledonia, Argyll, Dunoon, Benmore, ad River Eachaig, ad corticem *Alni*, 18 xi 1977, leg. *B. J. Coppins* 3256 (E-holotypus).

Thallus effuse, thin, ± smooth or finely scurfy-granular, pale grey-green, rather waxy in appearance; white, arachnoid, prothalline hyphae sometimes visible (×50). *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia usually numerous but occasionally few or absent, pallid to pale straw-brown or pale reddish brown; at first ± plane, adnate, ± immarginate but often with a white rim, *c.* 30–50 μm wide, from which a few white, arachnoid hyphae are sometimes seen to arise and penetrate into the thallus; later becoming convex although remaining adnate and never becoming constricted below; dispersed, or often confluent, and frequently coalescing to form large, irregular, waxy, nodulose clusters; individual apothecia 0·2–0·4(–0·6) mm diam, clusters up to 2 mm broad. *Hymenium* 35–40 μm tall, hyaline or dilute straw-yellow, K–. *Asci* clavate, 30–35×10–12 μm. *Spores* ellipsoid, ovoid, oblong-ellipsoid, oblong-ovoid or oblong, often slightly constricted at the septum, (0–)1-septate, 9–16×3–5 μm. *Paraphyses* numerous, branched and anastomosing, *c.* 1–1·5 μm wide and scarcely widening above; apices much branched and entangled. *Hypothecium c.* 40–120 μm tall, hyaline; hyphae hyaline, *c.* 1–2 μm wide, interwoven but becoming ± vertically orientated towards the hymenium, intermixed with short-celled ascogenous hyphae that are up to 5 μm wide. *Excipulum* well developed and clearly seen in young apothecia, *c.* 30–35 μm wide; hyphae radiating, branched and anastomozing, *c.* 1–2·5 μm wide.

Conidiomata of two types, one pycnidial, the other sporodochial. *Pycnidia* sometimes present but then usually few in number and inconspicuous, white, immersed, *c.* 40–60 μm diam; *conidiogenous cells* ± cylindrical, 6–10×1–1·5 μm; *conidia* (*mesoconidia*) cylindrical, sometimes faintly biguttulate, 4–5·3×1·2–1·5 μm. *Sporodochia* usually present, numerous and conspicuous, resembling small apothecia, white or pallid, pulvinate, 80–250 μm diam; *conidiogenous* cells cylindrical, 10–20×1·7–2 μm; *conidia* (*macroconidia*) cylindrical to oblong ellipsoid or occasionally oblong-obovoid, simple, eguttulate, 6·5–9·5×2·3–3 μm.

Chemistry: Thallus and apothecia K–, C–, PD–; no substances detected by t.l.c.

Observations: Micarea adnata is easily recognised by the combination of a pale grey-green, ± waxy thallus, pale, adnate to clustered apothecia and, above all, by the presence of sporodochia. These cushion-like conidiomata, which resemble small apothecia, produce conidia externally over their surface; such structures are unknown in any other *Micarea*, and appear not to have been previously reported for lichenised fungi. The rather large, non-septate, oblong conidia produced by the sporodochia are probably homologous to the curved or filiform and often septate macroconidia of such species as *M. cinerea, M. denigrata,* and *M. peliocarpa*. Some specimens of *M. adnata* have a few pycnidia with typical mesoconidia, but microconidia have not yet been found.

It is curious that this most distinctive species had not previously been afforded taxonomic recognition, although it was well known by Arnold who erroneously referred it to *Biatorina prasiniza*, a synonym of *M. prasina*. It is with forms of *M. prasina* with pallid apothecia that *M. adnata* is most likely to be confused. However, the former has a non-waxy, granular thallus composed of goniocysts, apothecia which soon become constricted below, usually smaller spores and an apparent absence of macroconidia. *M. prasina* is sometimes found to have pycnidia containing mesoconidia similar to those of *M. adnata*, but more frequently it has pycnidia containing microconidia. In addition, well developed specimens of *M. prasina* have one of three distinctive substances detectable by t.l.c., whereas *M. adnata* contains no lichen substances. *M. anterior* is similar to *M. adnata* in being lignicolous with pale apothecia and spores that are mainly 1-septate; however, its apothecia are usually darker, varying from a pale reddish or orange-brown to red-brown, with spores that are relatively narrower and ± fusiform, and a reddish brown excipulum. Furthermore, *M. anterior* has its mesoconidia borne in reddish brown, stalked pycnidia.

Habitat and distribution: M. adnata is usually found on old stumps and associated decaying bryophyte mats and peaty debris; the lignum of such stumps is usually soft and riddled with holes bored by insects. In addition, it is found on the loose bark of trunks of old trees, including *Alnus, Betula, Corylus, Quercus, Abies*, and *Pinus*. It usually occurs in extensive patches with few associated lichens, but amongst those noted are *Cladonia* spp. (including *C. coniocraea* and *C. squamosa*), *Micarea prasina, Parmelia laevigata*, and *Platismatia glauca*. Most collections are from old, ± natural deciduous or coniferous woodlands, but in western Scotland it is found also in old estate woodlands (possibly created from former ± natural woodland) containing many exotic trees.

The distribution of *M. adnata* in Britain is centred on western Scotland, with a few outlying localities in Cumbria and north Wales. It is so far unrecorded for south-west England or western Ireland, and it should be sought for in the old oak-woods of those regions. Its distribution coincides with an annual rainfall of over 1000 mm per year, distributed over at least 160 rain days, and is attributable to the General Western group of Coppins (1976). Similarly, many of its localities on mainland Europe are in regions with a high annual precipitation (over 1000 mm per year), viz. southern Bavaria, Austria (Steiermark), and Switzerland (Bern). However, there are a few specimens from lower rainfall districts, namely, middle and northern Bavaria, and eastern Sweden (Södermanland), perhaps in situations where local topographical or vegetational features provide a microclimate sufficient to compensate for the low rainfall. If the distribution of *M. adnata* is largely controlled by microclimatic conditions, usually resulting from a high rainfall, then it should be expected to extend to Norway, at least the south-western part of that country.

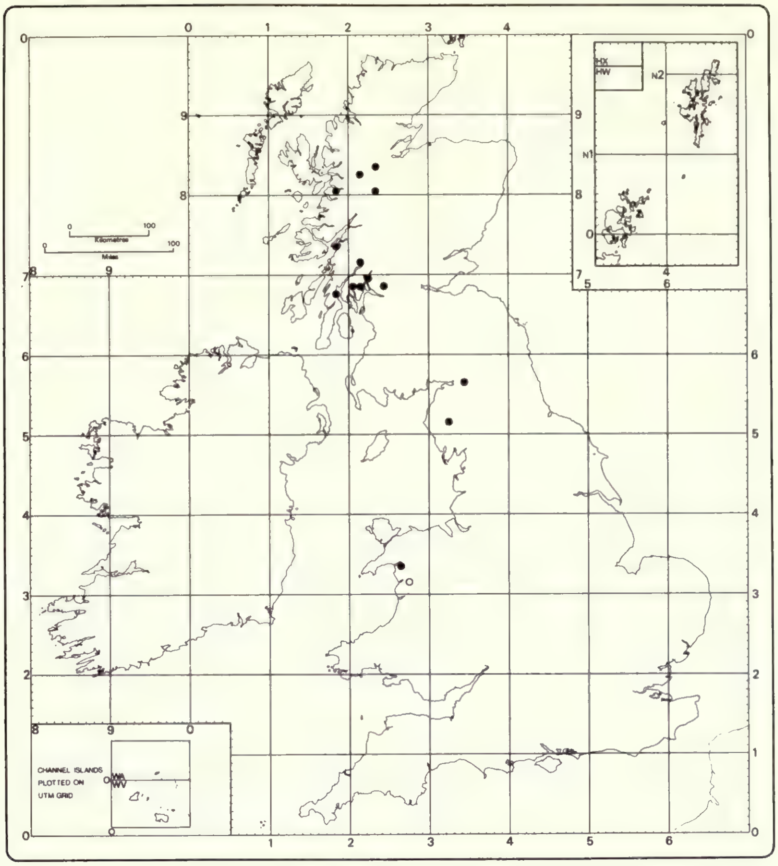
Exsiccata: Arnold *Lich. Mon.* 244 (BM ex K, M). Britzelmayer *Lich. Exs.* 174 (M).

2. **Micarea alabastrites** (Nyl.) Coppins
(Figs 2, 6, 8; Map 2)

in Topham & Walker in *Lichenologist* **14**: 66 (1982). –
Lecidea alabastrites Nyl. in *Flora, Jena* **62**: 207 (1879). – *Bilimbia sphaeroides* var. *alabastrites* (Nyl.) A.L. Sm., *Monogr. Br. Lich.* **2**: 138 (1911). Type: Ireland, West Galway, Derryclare, near Kylemore, on bryophytes on bark, 1878, *C. Larbalestier* (H-NYL 18656 – holotype!; BM – isotype!).

Thallus effuse, sometimes partly immersed in the substratum (especially when on lignum), but usually well developed on the surface of the substratum as crowded, confluent, ± convex-hemispherical to subglobose areolae. Areolae dull whitish, greenish white, or pale dull green, matt or slightly glossy, *c.* 40–140 μm diam, or up to 250 μm if containing a pycnidium of the macroconidial anamorph. Areolae in section, ecorticate but with a hyaline amorphous covering layer *c.* 4–10 μm thick.

Apothecia usually numerous and crowded, sometimes confluent and coalescing in groups of up to eight apothecia, adnate, plane to shallow-convex or convex-hemispherical, occasionally tuberculate, large, shallow-convex apothecia sometimes flexuose, often with an indistinct, slightly paler margin that is flush with the level of the disc, whitish, cream-white, ivory-white or pallid, 0·2–0·7 mm diam, or up to 0·9 mm diam when tuberculate. *Hymenium* 45–55 μm tall, hyaline, or dilute straw in upper part. *Asci* clavate, 42–50×12–16 μm. *Spores* fusiform or clavate-fusiform, sometimes slightly curved, 3(–5)-septate, occasional 7-septate spores encountered, (16–)18–26(–29)×(4–)4·5–5(–6) μm. *Paraphyses* numerous, branched, often anastomosing, *c.* 1–1·5 μm wide; apices often more richly branched and entangled, often slightly incrassate to 1·8 μm. *Hypothecium c.* 45–100 μm tall; hyphae interwoven, *c.* 1–1·7 μm; ascogenous hyphae with swollen cells *c.* 2–4 μm wide. *Excipulum* well developed (laterally *c.* 45 μ wide in young apothecia), hyaline, of richly branched and anastomosing, radiating hyphae, *c.* 1–1·5 μm wide.



Map 1 *Micarea adnata* ● 1950 onwards ○ Before 1950

Pycnidia usually present, white with hyaline walls, of two types: (a) immersed in areolae, *c.* 100–220 μm diam, ostiole often widely gaping; *conidia* (*macroconidia*) markedly curved, often sigmoid, sometimes faintly 3–5-septate, 21–55×*c.* 1 μm; (b) ± sessile, *c.* 50–100 μm diam, ostiole not, or only slightly gaping; *conidia* (*microconidia*) narrowly fusiform-cylindrical, 5–7×0·5–0·7 μm.

Chemistry: Thallus and apothecia C+ red; t.l.c.: gyrophoric acid.

Observations: M. alabastrites is morphologically and chemically very similar to *M. peliocarpa,* and it could easily be dismissed as representing a pale, shade form of that species. Apart from the complete absence of pigment from all its tissues, *M. alabastrites* is subtly different from *M. peliocarpa* in having slightly larger apothecia and spores. Shade forms of *M. peliocarpa* are usually sparingly fertile with scattered apothecia, whereas the apothecia of *M. alabastrites* are almost invariably numerous, crowded and often confluent. My early doubts regarding the distinction of these two species were dispelled by the collection, on several occasions, of *M. alabastrites* with adjacent thalli of *M. peliocarpa* with blackish apothecia; the slight differences in the sizes of apothecia and spores were confirmed with these collections. The two species also differ somewhat in distribution and habitat; *M. peliocarpa* is widely distributed throughout much of Europe on a wide range of substrata (tree trunks, mossy rocks peaty soil etc.); whereas *M. alabastrites* has a hyperoceanic distribution and occurs on tree trunks (or on bryophytes thereon) and occasionally lignum, but apparently never on mossy rocks or peaty soil.

In the recent checklist of British lichens (Hawksworth *et al.*, 1980) I mistakenly placed

Table 4 Diagnostic features for the separation of *Micarea alabastrites*, *M. cinerea*, and *M. peliocarpa*.

	peliocarpa	*alabastrites*	*cinerea*
Apothecia size (mm)	0·14–0·4(–0·6)	0·2–0·7	0·2–0·7
Apothecia colour	pallid to black	whitish or pallid	pallid to black
Hymenium height (μm)	40–55	45–55	55–70
Spore septation	(1–)3(–5)	3(–7)	(3–)7
Spore length (μm)	(11–)15–23(–24)	(16–)18–26(–29)	(19–)23–34(–38)
Spore breadth	3–5(–6)	(4–)4·5–5(–6)	4·5–6
Macroconidia shape	curved-sigmoid	curved-sigmoid	flexuose
Macroconidia length (μm)	21–40(–50)	21–55	50–110
Thallus colour	greenish white to dark blue-grey	greenish white or pale green	greenish white to dark blue-grey

'alabastrites' as a synonym of *M. cinerea.* At that time I had only seen the fragmentary isotype of *Lecidea alabastrites* in BM; I found this to have a few 7-septate spores and considered it a juvenile, shade-form of *M. cinerea.* Subsequent examination of the holotype (a large, healthy specimen) proved me to be wrong, and that it actually belonged to a hyperoceanic species which I had intended to describe as new to science. *M. cinerea* is another close relative of *M. alabastrites* and is more prone to occur with ± pallid apothecia than *M. peliocarpa*. It differs from both these species in having spores which are mostly 7-septate at maturity, and macroconidia which are flexuose and much longer; for a comparison of these three species see Table 4. Occasional 7-septate spores have been found in several specimens of *M. alabastrites*, but they never number more than two or three in each squash preparation.

M. alabastrites is one of the several lichens, named '*Bacidia* (or *Bilimbia*) *sphaeroides*' by British lichenologists. This name is based on *Lichen sphaeroides* Dickson, which is a species of *Biatora* Fr. (non Ach.) and currently known as *Catillaria sphaeroides* (Dickson) Schuler. The name *Bacidia sphaeroides* as commonly used by Scandinavian workers refers to a species (not known in Britain) which also belongs in *Biatora*; its correct name (basionym) is probably *Bilimbia tetramera* de Not.

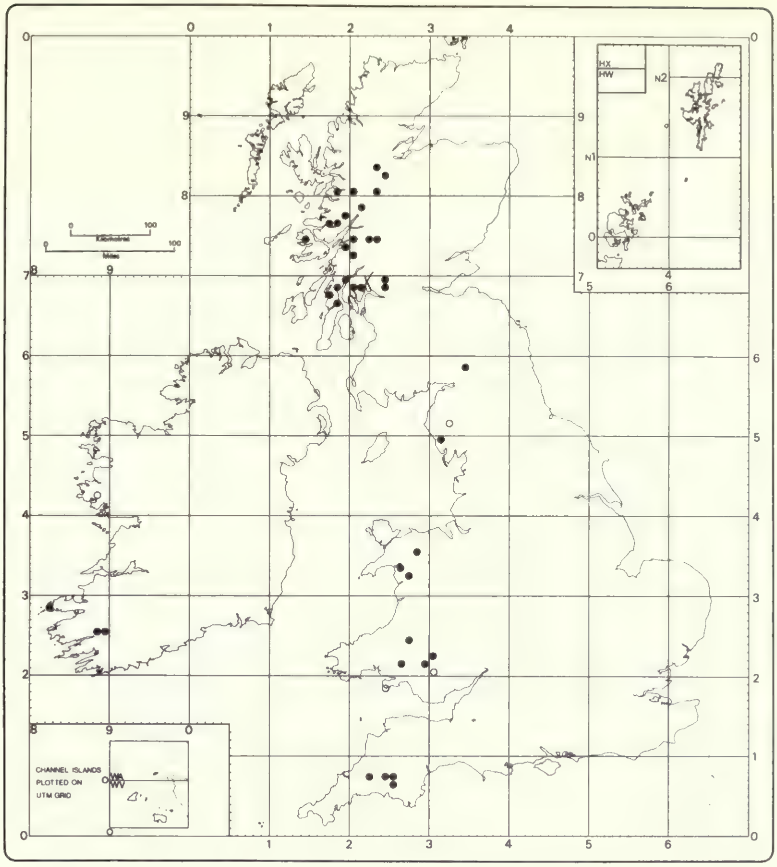
Habitat and distribution: In the British Isles *M. alabastrites* is mainly found in communities of the *Parmelietum laevigatae* association on the trunks of *Quercus, Betula,* and, more rarely, *Alnus, Fagus, Crataegus, Ilex, Pinus, Pseudotsuga*, and *Juniperus*. Associated lichens include *Bryoria fuscescens, Catillaria pulverea, Cladonia* spp., *Hypogymnia physodes, Lepraria incana* agg., *Micarea cinerea, M. peliocarpa, M. stipitata, M. synotheoides, Mycoblastus sanguinarius, M. sterilis, Parmelia crinita, P. laevigata, P. saxatilis, Platismatia glauca, Sphaerophorus globosus*, and *Usnea* spp. Occasionally it is found on lignum of fallen decorticate trunks, especially in the western native pinewoods; associated species include *Lecidea granulosa* agg., *Micarea lignaria, M. peliocarpa,* and *Platismatia glauca*. To date, it is not known to occur on mossy boulders, directly on rock, or on the ground on peaty debris, etc.

Its distribution in the British Isles is correlated with areas experiencing at least 180 'wet days' per annum and is referable to the 'General Western Group' of Coppins (1976). Elsewhere it is known from western Norway (Hordaland), the Azores (on *Cryptomeria*), and the Canary Islands (on *Erica arborea*).

3. **Micarea anterior** (Nyl.) Hedl.
(Figs 7B, 38C–D)

in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 76, 86 (1892). – *Lecidea anterior* Nyl. in *Flora, Jena* **58**: 299 (1875). – *Catillaria anterior* (Nyl.) Zahlbr., *Cat. lich. univ.* **4**: 29 (1926). Type: Finland, Tavastia australis, Asikkala, 1863, *J. P. Norrlin* (H-NYL 21655 – lectotype!; H – isolectotypes!).

Micarea anterior f. *diluta* Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 76, 86 (1892). Type: Sweden, Hälsingland, Järvsö, vii 1890, *J. T. Hedlund* (S – holotype!; UPS – isotype!).



Map 2 *Micarea alabastrites* ● 1950 onwards ○ Before 1950

Thallus effuse, endoxylic, or epixylic, then whitish and irregularly verrucose to 100 μm thick, sometimes becoming secondarily rimose, but without distinct primary areolae; in section, without an amorphous covering layer. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia numerous, few, or absent, immarginate, convex, adnate, often becoming tuberculate, pale reddish brown, dull orange-brown or red-brown, 0·15–0·35 mm diam, or to 0·6 mm when tuberculate, *Hymenium* 38–50 μm tall, ± hyaline with irregular, dilute red-brown (K−, or dulling) blotches, especially in upper part. *Asci* clavate or cylindrical-clavate, 35–45 × 10–12 μm. *Spores* oblong-ovoid to fusiform or ± bifusiform, often slightly curved, (0–)1(–2 or ?–3)-septate, 9–14(–16) × 2·5–4(–4·5) μm. *Paraphyses* rather numerous, simple or sparingly branched, many becoming much branched above with their apices entangled, 0·6–1 μm wide; apices often irregularly incrassate, hyaline and up to 1·5(–2) μm wide, or sometimes thickened with reddish brown pigment and up to 3 μm wide. *Hypothecium c.* 60–110 μm tall, hyaline. *Excipulum* thin but clearly seen in sections as a reddish brown reflexed zone; hyphae radiating, branched and anastomosing, hyaline and *c.* 1 μm wide, but becoming thickened with brownish pigment and up to 2 μm wide in the outer excipulum.

Pycnidia usually numerous; of two types: (a) sessile on old apothecia, but more usually borne on slender stalks (pycnidiophores) which arise from the thallus or in some cases from old apothecia; 70–250 μm tall and 40–70 μm diam (overall); stalks pallid but often with reddish brown blotches, glabrous, simple, or sometimes branched and bearing two or three pycnidia; pycnidia (excluding stalk) short cylindrical or slightly tapering inwards above, 40–80 μm tall and 40–70 μm diam, with dark reddish brown walls, K− or dulling; *conidia* (*mesoconidia*) cylindrical, often faintly biguttulate and slightly constricted in the middle, 3·5–4·5×1·2–1·6 μm; (b) sessile on the thallus or old apothecia, *c.* 30–40 μm diam, with dark reddish brown walls, K− or dulling; *conidia* (*microconidia*) narrowly cylindrical, (3·2–)3·6–4·5×0·7–0·9 μm.

Chemistry: Thallus K−, C−, PD−; sections of thallus and apothecia C−; no substances detected by t.l.c.

Observations: Micarea anterior is characterised by its reddish brown apothecia, rather narrow, mostly 1-septate spores, pale pycnidiophores bearing dark brown pycnidia, and a ± endoxylic, or thin and irregularly verrucose, thallus. Stalked pycnidia are a feature of several other lignicolous species (e.g. *M. melaeniza, M. misella, M. nigella,* and the occasionally lignicolous *M. botryoides*), but in those species the pycnidiophores appear black and have different pigmentations when examined microscopically. The pycnidiophores of *M. hedlundii* are brownish but distinctly tomentose, and those of the normally corticolous *M. pycnidiophora* and *M. stipitata* are entirely hyaline. *M. adnata* has its mesoconidia produced in immersed pycnidia and has macroconidia borne on small apothecia-like sporodochia; further distinguishing features from *M. anterior* include a ± waxy appearance of the whole plant, mostly paler apothecia, and relatively broader spores with rounded apices. Richly fertile specimens of *M. anterior* could be confused with *Catillaria erysiboides* (*q.v.*) but that species has marginate young apothecia, short ovoid spores, and a non-micareoid phycobiont.

Habitat and distribution: M. anterior is found on the rather soft and smooth lignum of decorticate trunks of *Picea* and *Pinus*, and associated with such species as *Cetraria pinastri, Cladonia* spp., *Hypogymnia physodes, Lecidea icmalea, Lepraria incana* agg., *Micarea adnata, M. contexta, M. misella, M. prasina, Parmeliopsis ambigua, P. hyperopta, Pertusaria pupillaris,* and the non-lichenised *Cryptodiscus pallidus*. It is a rare or overlooked species, apparently confined to Scandinavia, from where it is known from several localities in middle and southern Sweden, and south-west Finland.

Exsiccata: Malme *Lich. Suec.* 22 (M, S).

4. **M. assimilata** (Nyl.) Coppins, **comb. nov.**
(Fig. 9; Map 3)

Lecidea assimilata Nyl., *Lich Scand.*: 221 (1861). Type: Norway, Nordland, Helgeland, *M. N. Blytt* (H-NYL 16556 – lectotype!).
Lecidea assimilata a. [var.] *irrubata* Th. Fr., *Lich. Scand.* **2**: 522 (1874); *nom. inval.* (Art. 26).

Thallus growing on bryophytes, plant debris or sandy soil, composed of confluent, irregular, convex-verrucose, sometimes flattened and subeffigurate areolae that are often intermixed with cephalodia. Areolae white or brownish white, matt or sometimes glossy, 0·08–0·4 mm diam; in section, sometimes with a hyaline amorphous covering layer up to 7 μm thick, outermost hyphae hyaline; a ± algal-free medulla sometimes differentiated in large areolae. Thallus hyphae *c.* 1·8–3 μm diam. *Phycobiont* micareoid, cells 4–7 μm diam. *Cephalodia* often present, irregularly globose and hidden amongst the areolae, sometimes visible externally as brown areolae-like structures, 0·2–0·4 mm diam; containing *Nostoc,* cells 3–5 μm diam. Less often present are irregular, rather loose clusters (? cephalodia) of *Stigonema*.

Apothecia numerous, immarginate, convex to subglobose, matt or ± glossy (subnitid), 0·3–0·8 mm diam, sometimes forming tuberculate clusters up to 1·5 mm diam. *Hymenium,* 45–50 μm tall; upper part (epithecium) dark aeruginose, olivaceous or brownish-green, K−, HNO_3+ red; mid-hymenium dilute greenish; lower hymenium dilute greenish and K−, or dilute purplish and K+ purple intensifying or K+ sordid green. *Asci* clavate, 45–50×12–14 μm. *Spores* oblong-ellipsoid to oblong-fusiform, 0(–1)-septate, (10–)12–16(–19)×3–5 μm. *Paraphyses* numerous, simple below, but often forked or branched above, 1·5–1·7(–2) μm wide, sometimes widening above to 3 μm; apical walls hyaline although surrounded by densely pigmented gel-matrix. *Hypothecium c.* 150–400 μm tall, dark purple brown, K+ purple intensifying or (especially in upper part) K+ dark green; all parts HNO_3+ purple-red; hyphae interwoven but

± vertically orientated near the hymenium, *c.* 1·7–2·7 μm wide, embedded in a densely pigmented matrix; ascogenous hyphae *c.* 1·7–2·7 μm wide, embedded in a densely pigmented matrix; ascogenous hyphae *c.* 2·5–5 μm wide. *Excipulum* reflexed, mottled reddish brown or sordid olivaceous; hyphae radiating, branched and anastomosing, 1·5–2 μm wide.

Pycnidia rare, semi-immersed to sessile, black, 40–100 μm diam; walls dull reddish brown, or dull olivaceous in part; conidia (? microconidia) cylindrical, 6–9×1–1·5 μm.

Chemistry: Thallus K−, C−, KC−, PD−; t.l.c.: no substances.

Observations: Micarea assimilata is characterized by its conspicuous, whitish, verrucose areolae which are often intermixed with brown cephalodia, rather large, convex, black apothecia, green (K−) epithecium, dark purple-brown hypothecium and predominantly simple, large spores. It is apparently closely related to *M. crassipes, M. incrassata, M. melaenida*, and *M. subviolascens*, all of which share rather stout, simple or sparingly branched paraphyses, rather stout excipular hyphae, dark hypothecia and an absence of lichen substances. In many ways *M. assimilata* is identical to *M. incrassata* and both occur in similar habitats; indeed the latter has often been considered a variety (var. *infuscata*) of the former (e.g. Anderson, 1964; Hertel, 1977). However, *M. incrassata* differs in several respects, the most important of which is its quite different, red-brown hypothecium which lacks any trace of purple pigmentation in water, K or HNO_3. In addition, it has an often darker thallus, less prominent apothecia and a generally higher proportion of septate spores. *M. subviolascens* is similar in appearance to *M. assimilata*, but grows on rock and has a green, K+ violet epithecial pigment. *M. melaenida* differs from the last three species in its comparatively small apothecia and less conspicuous thallus, absence of green pigmentation in apothecial tissues, preponderance of 1-septate spores, shorter conidia, and confinement to argillaceous, or fine-grained, mineral soils. *M. crassipes* occurs in much the same habitats as *M. assimilata* and the two species have been much confused. However, *M. crassipes* is easily distinguished by its apothecia which are thinly marginate (at least when young) and markedly constricted below, often being turbinate or even short-stipitate; also by its thallus which is composed of small granular-areolae which sometimes proliferate to give it an isidiose appearance. In section, the apothecia of *M. crassipes* display a well-developed excipulum and a distinctly two-zoned hypothecium.

Pycnidia are rare and difficult to find in members of the *M. assimilata* group, and have not yet been found at all in *M. subviolascens*. The remaining species appear to have one conidium type only; although the conidia are rather large, they are probably microconidia. However, the relatively shorter and broader conidia of *M. crassipes* may be better described as mesoconidia.

Cephalodia are here reported from *M. assimilata* and *M. incrassata*, apparently for the first time. In both cases the blue-green alga concerned is *Nostoc*, which loses its filamentous form. In addition, irregular clusters of partially disrupted *Stigonema* filaments are sometimes present amongst the areolae of *M. assimilata, M. incrassata,* and also *M. subviolascens*. Hyphae, presumably belonging to the lichens, are seen to ramify through these clusters; but whether or not these loosely organised structures can be considered to be cephalodia is a problem requiring further detailed anatomical and experimental investigation. Cephalodia or cephalodia-like structures have not been encountered in any other *Micarea* species.

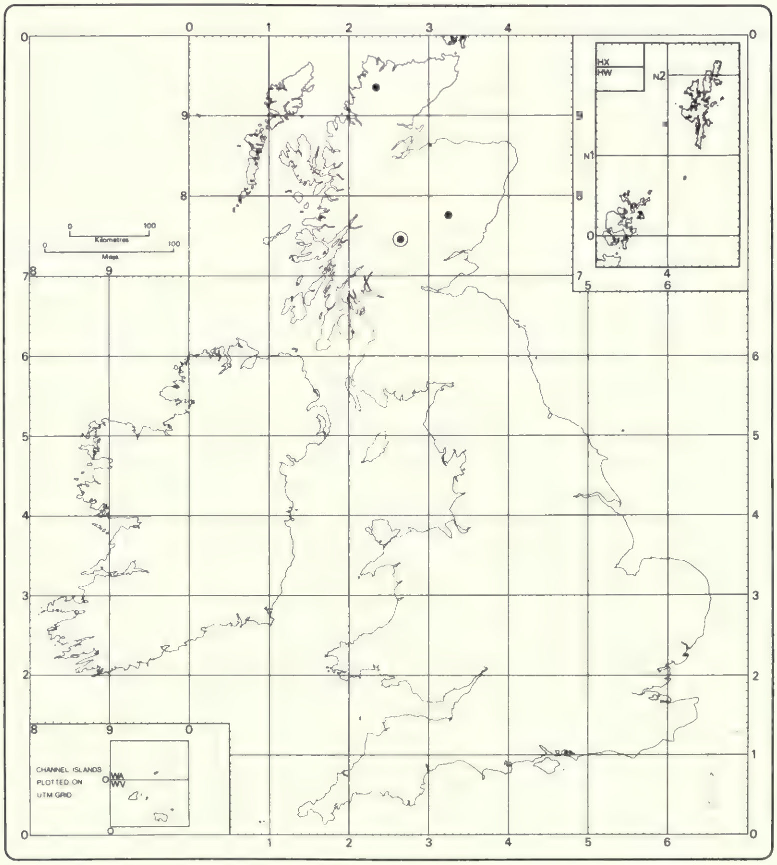
The closely related *Lecidea limosa* Ach. and *L. stenotera* (Nyl.) Nyl. have often been confused with *M. assimilata* and *M. incrassata*, but they can be distinguished by their pale hypothecia, paraphyses which are individually supplied with a dense, hyaline, gelatinous sheath, and more organised excipular structure. Together with *Catillaria contristans* (Nyl.) Zahlbr. they probably represent a distinct genus within the *Lecideaceae*, although perhaps not far removed from *Micarea*. In British herbaria (at least) there has been much confusion between *M. assimilata* and *Lecidea hypnorum* Lib. The latter has marginate, brown-black apothecia, simple paraphyses, 0(–3)-septate spores which become straw coloured and finely warted with age, a reddish brown excipulum composed of radiating, stout, pachydermatous, heavily conglutinated hyphae, *c.* 3–5 μm wide, and bears little resemblance to a *Micarea*. In addition, the hymenium, hypothecium and excipulum of *L. hypnorum* (and the related *L. berengeriana* (Massal.) Th. Fr., and *L. sanguineoatra* auct.) often contain minute granules of a dark violet (K+ aeruginose) pigment.

More understandable cases of mistaken identity involve *Lecidea caesioatra* Schaerer, which bears a close superficial likeness to *M. incrassata*. It can be distinguished from this *Micarea* by its dark blue-grey apothecia which have a caesious bloom when wet, excipulum of conglutinated (in K) hyphae, and non-micareoid phycobiont with cells *c.* 8–12 μm diam.

Habitat and distribution: M. assimilata grows on decaying bryophytes and plant detritus on the ground or on soil accumulation in rock crevices in arctic (i.e. low altitudes at high latitudes) or montane situations. The realisation that this species belongs in *Micarea* came so late in the present study, that I have been able to examine only a limited amount of herbarium material. To date, I can confirm its presence in northern Scandinavia and the single outlying locality in Scotland. Specimens purporting to be *Lecidea assimilata* from the Alps and other central European mountains have proved to be *M. crassipes, M. incrassata,* or *'Lecidea'* species not referable to *Micarea*. Material of '*Lecidea assimilata*' from Greenland distributed as Hansen *Lich. Groenland Exs.* 172 and 247 belongs to *Lecidea stenotera* and *L. limosa* respectively.

The Scottish locality is Ben Lawers in Perthshire, a mountain long renowned for its arctic-alpine flora (Anon, 1972; James, 1965*b*). *M. assimilata* was collected there by W. L. Lindsay in 1856. Recent collections from Ben Lawers, and other Scottish localities, are referable to other species, such as *Lecidea caesioatra, L. hypnorum, L. limosa,* and *Micarea incrassata*.

Exsiccata: Krypt. Exs. Vindob. 2268 (BM, H). Malme *Lich. Suec.* 216 (H).



Map 3 *Micarea assimilata* ◉ Before 1950 + *Micarea incrassata* ● 1950 onwards

5. **Micarea bauschiana** (Körber) V. Wirth & Vězda (Figs 5, 10A, 40D; Map 4).

in Vězda & V. Wirth in *Folia geobot. phytotax., Praha* **11**: 95 (1976). – *Biatora bauschiana* Körber, *Parerga lich.*: 157 (1860). – *Lecidea bauschiana* (Körber) Lettau in *Hedwigia* **55**: 28 (1914). Type: Germany, Baden-Württemberg, Baden-Baden, on the way to Yburg, on porphyry, 1859, *Bausch,* Rabenh. *Lich. Eur.* 648 (M – lectotype!, sel. V. Wirth & Vězda (*loc. cit*); M – isolectotype!); additional isotype material distributed as Arnold *Lich. Exs.* 120 (BM!, M!).

Lecidea infidula Nyl. in *Flora, Jena* **51**: 475 (1868). Type: Jersey, *C. Larbalestier* (H-NYL p.m. 5413 – holotype!).

Lecidea lynceola Th. Fr., *Lich. Scand.* **2**: 561 (1874). Type: Norway, Christiana [Oslo], Tveten, 20 v 1868, *N. G. Moe* 257 (UPS – holotype!).

Lecidea semipallens Nyl. in *Flora, Jena* **59**: 234 (1876). Type: Ireland, West Galway, Lough Inagh, 1875, *C. Larbalestier* (H-NYL 19399 – lectotype!; isolectotypes: BM ex K!, H-NYL 19402!).

Lecidea dilutiuscula Nyl. in *Flora, Jena* **59**: 308 (1876). Type: England, South Devon, near Buckfastleigh, *H. B. Holl* (BM – lectotype!; H-NYL 10754 – isolectotype!).

Lecidea rusticella Nyl. in *Flora, Jena* **61**: 245 (1878). Type: Ireland, West Galway, Connemara, Tullywee Bridge, 1876, *C. Larbalestier* (H-NYL 20206 – holotype!; topotypes ['1878']: BM!, BM ex K!).

?*Lecidea callicarpa* Larbal. ex Leighton, *Lich. Fl. Br.*, ed. 3: 266 (1879). Type: Ireland, West Galway, Glencorbot near Kylemore, 1877, *C. Larbalestier* (not seen; possibly in BM (incl. BM ex K) but not traced).

?*Lecidea semipallens* var. *obscurior* Lång ex Havaas in *Bergens Mus. Årb.* **1935**(2): 27 (1935). Type: Norway, Dalsbø, 1903, *J. J. Havaas* (not seen; not traced in BG or H).

?*Catillaria microspora* Maslova in *Ukr. bot. Zh.* **30**(5): 665 (1973). Type: USSR, Regio Volhyniensis, distr. Ljuboml., in pineto haud procul pag. Kamenca, ad saxa granitica, 11 vi 1969, *W. R. Maslova* (KW – holotype, not seen; but a slide prepared from the holotype by H. Kilias examined).

Thallus thin (<100 μm thick), slightly uneven, continuous or finely rimose, usually becoming scurfy-granular and then often thicker (to *c.* 300 μm thick), but never forming discrete areolae or goniocysts, greenish grey, grey-green or pale grey-brown, sometimes 'oxydated' and then pale ochraceous or ferrugineus; often obscured by a pale green (white in old herbarium specimens) covering of free-living algae. Thallus in section, ecorticate, without an amorphous hyaline covering layer; outermost hyphae hyaline and without surrounding pigment. *Phycobiont* not micareoid; cells thin-walled, ± globose, 5–12 μm diam.

Apothecia numerous, immarginate and convex-hemispherical from the start, mostly becoming subglobose or tuberculate, 0·2–0·3 mm diam, or up to 0·7 mm diam when tuberculate; very variable in colour, from pale bluish grey (sometimes pallid in part and then 'piebald') to dark bluish grey to black, shade forms pallid or pale brown; brown colouration often due to the infestation of ascocarp tissues by a dematiaceous hyphomycete (?*Bispora* sp.). *Hymenium* (35–)40–50(–60) μm, sometimes hyaline throughout (shade forms), more usually dilute greenish, olivaceous or aeruginose and often more intensely pigmented in the upper part, K−, HNO_3+ red. *Asci* cylindrical-clavate, 35–50×9–12 μm. *Spores* ellipsoid or ovoid-ellipsoid, simple, 6·5–10·5×2·5–4 μm. *Paraphyses* rather scanty, of two types: *p.p.* evenly distributed, sparingly branched and anastomosing below, septa indistinct, 0·8–1·2 μm wide, often very thin ('stretched') in the lower hymenium of old, much expanded apothecia; apical parts usually branched and sometimes incrassate (to 2 μm wide); *p.p.* fewer in number, as scattered individuals or in small fascicles, straight, simple or occasionally forked above, distinctly septate, stout, *c.* 1·5–2 μm wide; apices swollen (up to 4 μm wide) and often cemented together (when in fascicles) by deeply pigmented matrix. *Hypothecium c.* 80–150 μm tall, hyaline, or dilute greenish or dilute brownish olive (K−, HNO_3+ reddish) in upper part; hyphae interwoven, but becoming vertically orientated toward the hymenium, hyaline, *c.* 1–2 μm wide; pigment when present confined to the gel-matrix and not closely adhering to the hyphae; ascogenous hyphae with swollen, cells *c.* 2–5 μm wide. *Excipulum* not evident even in sections of young apothecia; part of the hymenium is often reflexed to below the hypothecium to give the appearance of an excipulum.

Pycnidia often present, immersed, *c.* 40–80 μm diam; walls greenish K−, HNO_3, + reddish, or rarely hyaline (shade forms); *conidiogenous cells* irregularly subcylindrical, 6–9×1–1·4 μm, often with a swollen base up to 3 μm wide; *conidia* (*microconidia*) cylindrical, eguttulate, 4–6×0·8–1 μm. A few collections with pallid apothecia have associated pycnidia, *c.* 60–100 μm diam, with hyaline walls and containing (often biguttulate) *mesoconidia* 2·8–4·3×1–1·3 μm (see 'Observations' below).

Chemistry: All parts K−, C−, KC−, PD−; no substances detected by t.l.c.

Observations: Micarea bauschiana is closely related to, and often confused with, *M. sylvicola* (*q.v.*), and the two species often grow together. *M. bauschiana* is notoriously variable in the colour of its apothecia, but the full range of variation from pallid to blackish can be seen over small distances (a few centimetres) in a single population (Fig. 5: p. 30) and the variation appears to be solely phenotypic.

When growing on iron-rich rocks the thallus of *M. bauschiana* is often oxydated. In a few specimens (including types of *Lecidea rusticella*) this oxydation has extended to the apothecia in which finely granular, ferruginous material has been deposited (especially in the epithecium and hypothecium); such specimens have been confused with *M. lutulata* and species of *Protoblastenia*.

A few collections from Austria and Scotland (considered here as *M.* cf. *bauschiana*) have entirely pallid apothecia which are accompanied by pycnidia containing mesoconidia (see description above). Such pycnidia have not been detected in specimens of *M. bauschiana* with pigmented apothecia, and it is possible that the former collections represent a distinct taxon. However, one of these collections (Austria, Steiemark, Graz, Schöckl N of St Radegund, 1978, *Poelt* (GZU) also has typical (for *M. bauschiana*) microconidia-containing pycnidia, and it may be that there is some environmental control (e.g. a response to very low light intensities) involved in the initiation of the mesoconidial anamorph. Further careful field observations and laboratory studies are required to establish the status of these seemingly anomalous collections.

Forms of *M. bauschiana* (*s. ampl.*) with pallid apothecia should be compared with the much rarer *M. lithinella* (*q.v.*) which can be distinguished by its micareoid phycobiont. In addition, *M. lithinella* seems not to occur in the ombrophobous, aerohygrophilous *Micareetum sylvicolae*, and is a rather ombrophilous, substratohygrophilous species of damp, shaded rocks or stones. However, I must stress that this ecological interpretation of *M. lithinella* is based on the limited data available from the herbarium specimens and requires confirmation by field studies.

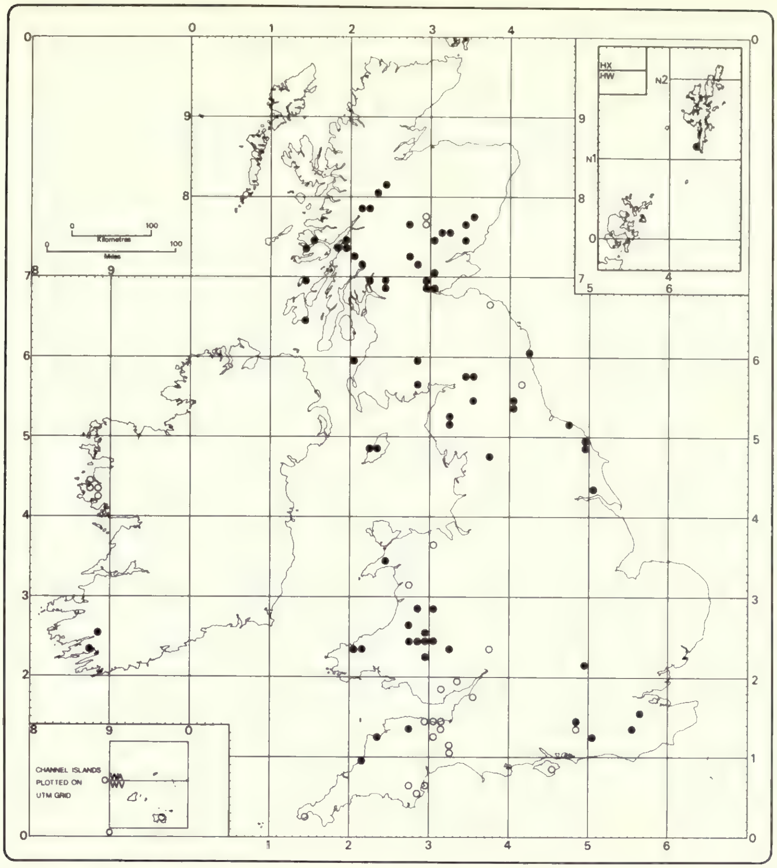
Material recently distributed as '*M. bauschiana*' in Hertel *Lecid. exs.* no. 54 is not this species. It has weakly marginate apothecia due to a well developed excipulum, and a large-celled (9–17 μm diam) phycobiont, the cells of which are deeply penetrated by distinct haustoria (as in *M. intrusa*). It is probably an undescribed species of *Micarea* and will be treated in a later publication following more critical studies.

Habitat and distribution: M. bauschiana is a faithful member of the *Micareetum sylvicolae* and grows on rocks, stones, roots, and consolidated soil in dry underhangs in woodlands or sheltered valleys. In the British Isles *M. bauschiana* is the commonest member of the *M. sylvicola* group. It is particularly common in the north and west but also occurs in suitable situations (e.g. dry stones in sandy banks in woodlands) in the lowlands of south-west England. It seems to be widely distributed in Europe but I have not seen enough specimens to make an assessment of any distributional tendencies. It occurs in the Azores and the Canary Islands, but I have not seen any additional material from outside Europe.

Exsiccata: Arnold *Lich. Exs.* 120 (BM, M), 1233 (M). Johnson *Lich. Herb.* 434 *p.p.*, 504 (HAMU). Larbal. *Lich. Herb.* 68 (BM), 305 *p.p.* (LD). Rabenh. *Lich. Eur.* 648 *p. max. p.* (M). Zwackh *Lich. Exs.* 279A–B, 594A–B, 595 (M).

6. **Micarea botryoides** (Nyl.) Coppins
(Figs 10b, 35, 38A; Map 5)

in D. Hawksw., P. James & Coppins in *Lichenologist* **12**: 107 (1980). – *Lecidea apochroeella* var. *botryoides* Nyl. in *Flora, Jena* **50**: 373 (1867). – *Lecidea botryoides* (Nyl.) Zahlbr., *Cat. lich. univ.* **3**: 740



Map 4 *Micarea bauschiana* ● 1950 onwards ○ Before 1950

(1925). Type: Finland, Tavastia australis, Lammi, Evo, Lapinkallio, 1866, *J. P. Norrlin* 404 (H-NYL 20685 *p.p.* – lectotype!; H – isolectotype!).

Note: In the protologue Nylander states 'ad lignum putridum' but this is clearly an error (see Vainio 1934: 361). The lectotype has been selected from a packet in the Nylander Herbarium containing two pieces of rock – one with *M. lutulata*, the other (lectotype) with the apothecia and characteristic stalked pycnidia of *M. botryoides*. It is possible that Nylander's diagnosis was based in part on the apothecia of *M. lutulata*, which bear many similarities to those of *M. botryoides*. Because Art. 70 of the ICBN is no longer applicable *Lecidea apochroeella* var. *botryoides* cannot be rejected as being based on discordant elements; consequently the part containing *M. lutulata* is excluded, and that part including stalked pycnidia (as described in Nylander's diagnosis) is chosen as the lectotype.

Thallus effuse, thin, more rarely developing into a thick, loose crust up to *c.* 0·4 mm thick, scurfy-granular, pale to dark dull green, dark olive-green, or dull greenish black, sometimes whitish buff when on dry, deeply shaded rocks. When very thin the thallus consists of flattened granules, *c.* 20–50 μm diam., which are often dispersed and interconnected by white, arachnoid, prothalline hyphae. Thickening of the thallus is caused by the production of goniocysts (*c.* 16–30 μm diam), the first of which appear to arise by budding from the primary granules; when thick the thallus has a ± gelatinous appearance when wet. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia usually few, more commonly absent, immarginate, at first convex-hemispherical, soon becoming ± globose and much constricted below (sometimes short-stipitate), often becoming tuberculate, black, or dark brown (in deep shade), matt, 0·1–0·25 mm diam, or to 0·5 mm when tuberculate. *Hymenium* 25–35 μm tall, hyaline or sometimes tinged dilute brown (K−, HNO_3−) or dilute olivaceous (K−, or K± green intensifying, HNO_3+ red) in places, but always with numerous dark brown (K± olivaceous tinge, HNO_3± reddish tinge) vertical streaks. *Asci* cylindrical-clavate or clavate, 20–35×7–9 μm. *Spores* ovoid, oblong-ellipsoid or oblong-ovoid, straight or slightly curved, 0–1(–3)-septate, 8–13(–16)×2·3–3·7(–4) μm. *Paraphyses* rather scanty, of two types: *p.p.* evenly distributed, flexuose, simple or sparingly branched, sometimes anastomosing, thin, 0·7–1 μm wide, sometimes widening above to 1·7 μm, walls hyaline throughout; *p.p.* fasciculate, simple or sparingly branched, stout, *c.* 2–2·5 μm wide, sometimes widening above to 3·5 μm, coated ± throughout by dark brown pigment. *Hypothecium c.* 60–120 μm tall, dark reddish brown, K− or dulling, HNO_3− or red tinge slightly intensifying; hyphae coated with dark brown pigment, *c.* 2–3 μm wide, interwoven but becoming vertically orientated towards the hymenium and sometimes continuing into it as stout, fasciculate, pigmented paraphyses; ascogenous hyphae similarly pigmented, with short, swollen cells to 5 μm wide. *Excipulum* indistinct, sometimes evident in young apothecia as a reflexed reddish brown zone concolorous with, or slightly paler than, the hypothecium; hyphae radiating, branched and anastomosing, *c.* 1–1·5 μm wide, their walls sometimes with a thin coating of brown pigment.

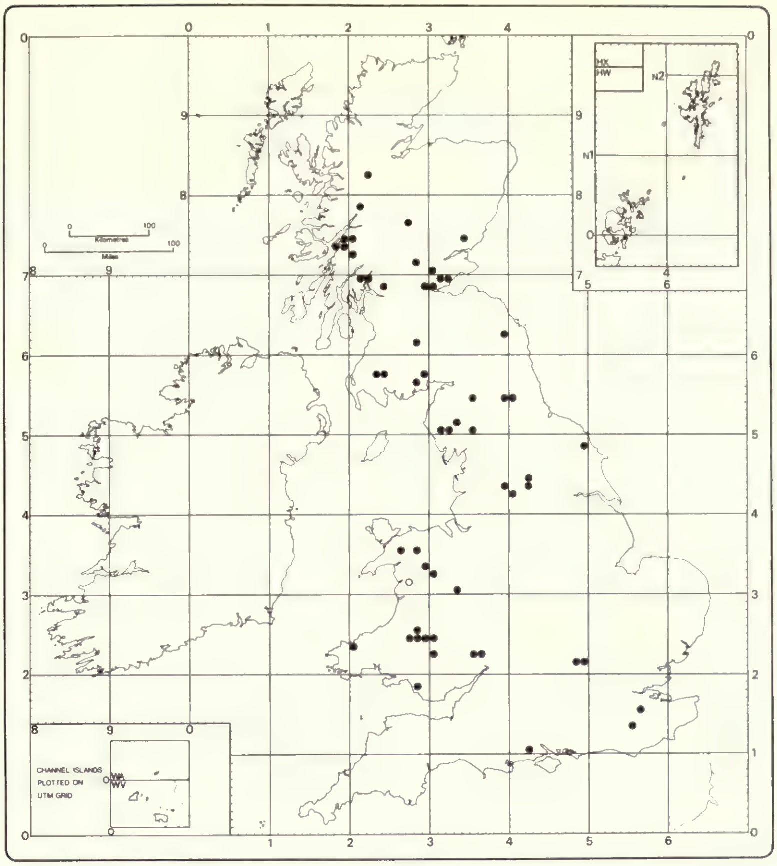
Pycnidia always present and numerous, sessile or, more usually, distinctly stalked, black, 50–400 μm tall (including stalk) and 40–90 μm diam; stalks simple, or branched and bearing up to six pycnidia; the 'stalk-part' below the current conidia-producing pycnidia often includes old pycnidia (see Fig. 35); the stalk and pycnidia are usually black but in extreme shade forms the stalk tissue may be ± colourless, contrasting with the dark brown or blackish, current and old pycnidia. In microscope preparations (at ×400): pycnidiophore tissue dilute to dark fuscous or reddish brown, K− or dulling, HNO_3− or red tinge slightly intensifying; pycnidial wall dark greenish brown, K− or K+ green intensifying HNO_3+ red. *Conidiogenous cells* ± cylindrical or elongate ampulliform, often with swollen base which is thickened with brownish pigment, often with one or two percurrent proliferations, 3·5–7·5×1–1·4 μm, base sometimes swollen to 2·5 μm wide. *Conidia* (*mesoconidia*) ± cylindrical, often biguttulate, sometimes slightly constricted in the middle, 3·5–4·8×1–1·5 μm.

Chemistry: Thallus K−, C−, PD−; sections of apothecia and thallus C−; no substances detected by t.l.c.

Observations: Micarea botryoides is easily recognised by its numerous, black, stalked pycnidia, whose walls are dark greenish brown (K− or K+ green intensifying), and its normal occurrence on substrate other than lignum. It is very similar to the rare *M. melaeniza*, but that species has shorter conidia, smaller, simple spores, and is apparently confined to lignum. *M. misella* often has stalked, black pycnidia, but is usually lignicolous. However, it does occasionally occur on decaying bryophytes where it could be confused with *M. botryoides*. In such instances their separation is easy because the pycnidia of *M. misella* contain an olivaceous or dull brownish pigment that turns violet in K. When on rock the apothecia of *M. botryoides* could be confused with those of *M. lutulata*, but the latter species has smaller, simple spores, a non-micareoid phycobiont, and immersed pycnidia. When on soft lignum it should be compared with *M. nigella* which is superficially identical, but has a purple-brown (K+ green) pigment in its apothecia and pycnidia.

Sterile forms of *M. botryoides* have puzzled lichenologists for many years, being dismissed with such remarks as 'indeterminate pycnidia' or 'fungus'. In 1867 Leighton distributed sterile material of *M. botryoides* in his exsiccate (no. 388), as '*Lecidea sabuletorum* var. *milliaria* (Fr.), spermagonia', evidently believing it to be the pycnidial state of *Micarea lignaria,* the apothecia of which occur on some of his specimens. The identity of these pycnidia remained a mystery until my discovery of fertile material in Scotland in 1976 and my subsequent examination of the type material of *Lecidea apochroeella* var. *botryoides* in 1979.

Habitat and distribution: M. botryoides is usually found as a constituent of the *Micareetum sylvicolae* in dry underhangs, growing on solid rock, loose stones, consolidated soil, tree roots, and loose mats of moribund bryophytes; but it also occurs on rock, stones, and decaying bryophytes in wetter shaded situations. There are a few collections made from the soft,



Map 5 *Micarea botryoides* ● 1950 onwards ○ Before 1950

crumbling lignum of old stumps, but I have not seen it on the firmer, ± smooth lignum favoured by *M. melaeniza* and *M. misella*. In the environs of some industrial regions (e.g. the West Yorkshire conurbation) it has been found on bark at the bases of trunks of *Acer* and *Betula* in sheltered woodlands.

M. botryoides is a widespread species, especially in western and upland regions of Britain, and is certainly much more common than current records would suggest. Several of these records result from accidental gatherings, being subsequently identified on samples of other members of the *Micareetum sylvicolae*. This gives an indication as to how often this species must have been overlooked. It is little recorded outside Britain, and to date I know it only from Norway (Sör-Tröndelag and Hordaland), Finland (Tavastia australis), and north-west France.

Exsiccata: Leighton *Lich. Brit.* 388 (BM, BON, DBN, E, M).

7. **Micarea cinerea** (Schaerer) Hedl.
(Figs 11, 39; Map 6)

in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 81, 93 (1892). – *Lecidea cinerea* Schaerer, *Lich. Helv. spic.*, sect. 3: 156 (1826). – *Bacidia cinerea* (Schaerer) Trevisan in *Linnaea* **28**: 293 (1856). – *Bilimbia cinerea* (Schaerer) Körber, *Parerga Lich.*: 164 (1860). Type: Switzerland, 'ad infimos Abietum truncos, in sylva Konitz', *L. E. Schaerer* (G – holotype!; M – ? isotype!).

Lecidea sphaeroides var. *albella* Schaerer, *Lich. Helv. spic.*, sect. 4–5: 165 (1833). Type: Switzerland: 'Schweiz' [on conifer bark], *L. E. Schaerer* (M – neotype!). See note (i).

Biatora delicatula Körber, *Denkschr. Feier ihres fünfzigjäh. Best. herausg. Schles. Gesellsch. vater. Kult.*, *Breslau*: 233 (1853). – *Bilimbia delicatula* (Körber) Körber, *Syst. lich. Germ*: 212 (1855). Type: lectotype as for *Lecidea sphaeroides* var. *albella* Schaerer. See note (ii) below.

Bilimbia cinerea f. *hypoleuca* Stizenb. ex Arnold in *Flora, Jena* **58**: 598 (1864). – *Micarea cinerea* f. *hypoleuca* (Stizenb. ex Arnold) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 82, 93 (1892). Type: Germany, Bayern, near Eichstätt, Affenthale, on young *Picea abies* in a wood, viii 1864, *F. C. G. Arnold* (M – lectotype!).

Notes. (i) No material labelled *Lecidea sphaeroides* var. *albella* could be traced in G (Geissler, *in litt.*) and an undated specimen in M is selected as neotype. If it can be proven that this specimen was collected before 1833, it should be regarded as a lectotype.

(ii) No material referred to in the protologue of *B. delicatula* has been traced in L, WRSL or elsewhere. However, Körber gives 'Lecidea sphaeroides α albella Schaer. Enum. 193.' as a synonym. This citation refers to Schaerer (1850) and is an indirect reference to *Lecidea sphaeroides* var. *albella* Schaerer (1833). Consequently I have typified both names with the same specimen in M.

Thallus effuse, sometimes partly immersed in the substratum (especially when on lignum), more usually developed on the surface of the substratum as rounded, shallow-convex, hemispherical or ± globose areolae. Areolae scattered to ± contiguous, smooth, greenish white to blue-grey, or more rarely becoming dark grey, often dark coloured on upper surface but greenish white below, *c.* 40–160 μm diam or up to 300 μm diam if containing a pycnidium of the macroconidial anamorph. Areolae in section, ecorticate but with a hyaline amorphous covering layer *c.* 2–5 μm thick; outermost hyphae often with grey-green to aeruginose walls, K−, HNO_3+ red. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia usually numerous (see 'observations'), adnate, plane to convex, sometimes becoming tuberculate, sometimes with an indistinct margin that is ± flush with the level of the disc, pale leaden-grey to grey-black (margin often paler), or ivory-white or pallid in shade forms, (0·2)0·3–0·7 mm diam or up to 1·3 mm when tuberculate. Disc matt and finely roughened, but margin smooth and often ± glossy. *Hymenium* 55–70 μm tall, hyaline, but usually olivaceous or aeruginose (K−, HNO_3+ red) in upper part (epithecium). *Asci* clavate 50–65×15–20 μm. *Spores* fusiform, often slightly curved, (3–)5–7-septate, (19–)23–34(–38)×4·5–6 μm. *Paraphyses* numerous, branched and often anastomosing, 1–1·4 μm wide; apices often more richly branched and entangled, often slightly incrassate to *c.* 1·8 μm, or 2·5 μm due to thickening by greenish pigment. *Hypothecium c.* 40–70 μm tall, hyaline; hyphae interwoven, *c.* 2–4 μm wide. *Excipulum* well developed, hyaline or pale straw, or richly branched and anastomosing hyphae, *c.* 1–1·5 μm.

Pycnidia frequently present, of two types: (a) immersed in areolae, white or faintly greenish around the ostiole, 160–300 μm diam, ostiole often widely gaping; *conidia* (*macroconidia*) ± straight or flexuose, filiform, 9–17-septate, 50–110×*c.* 1 μm; (b) ± sessile, white, *c.* 40–70 μm diam, ostioles not, or only slightly, gaping; *conidia* (*microconidia*) narrowly fusiform-cylindrical (3·8–)4–5×0·5–0·7 μm.

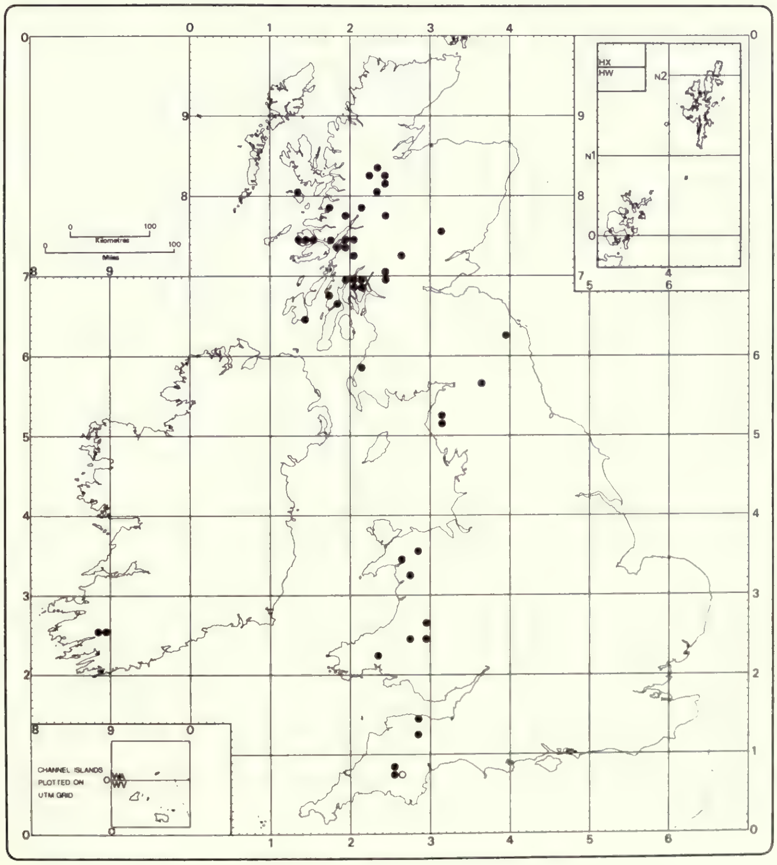
Chemistry: Thallus and whitish apothecia K−, C+ red, PD−; apothecia in section C+ red; t.l.c.: gyrophoric acid.

Observations: M. cinerea is very variable with regard to the colour of its apothecia and thallus; as with *M. peliocarpa* this variation is due to the amount of green pigment produced in response to environmental factors, especially light. Morphologically and chemically *M. cinerea* is closely allied to *M. alabastrites* and *M. peliocarpa*; the diagnostic features of each of these three species are compared in Table 4. Forms of *M. cinerea* with blackish apothecia can be confused with *M. lignaria* (including var. *endoleuca*) but on close inspection the latter will be seen to differ in its ± globose apothecium with a poorly differentiated excipulum (in vertical section), usually brownish or greenish upper hypothecium, less strongly branched paraphyses and chemistry.

M. cinerea is usually well fertile with numerous apothecia, but sterile forms with numerous macroconidia-containing pycnidia have been encountered; the macroconidia are about twice as long as those found in *M. peliocarpa* and *M. alabastrites* and so are readily identifiable (see 'Key to species without apothecia, pp. 107–108).

Habitat and distribution: In the British Isles *M. cinerea* is mostly found in communities of (or closely akin to) the *Parmelietum laevigatae* on the trunks or over bryophytes thereon of *Quercus, Betula* and, less often, *Alnus, Corylus, Fraxinus, Ilex, Sorbus, Larix, Pinus*, and *Pseudotsuga*. Associated species in these communities include *Catillaria pulverea, Cladonia coniocraea, C. macilenta, C. squamosa, Haematomma caesium, H. elatinum, Lecidea icmalea, Lepraria incana, Micarea alabastrites, M. stipitata, M. synotheoides, Mycoblastus sterilis, Parmelia laevigata, P. saxatilis, Platismatia glauca, Stenocybe septata, Thelotrema lepadinum, Trapelia corticola ined.*, *Frullania tamarisci, Lejeunea ulicina, Scapania gracilis, Dicranum fuscescens*, and *Hypnum cupressiforme*. Less commonly it is found in the lignum of fallen, decorticated trunks. Occurrences on other substrata are rare although I have found it on one occasion growing directly on rock (Coed Hafod in Denbigh) where it was associated with *Trapelia involuta* on the top of a dry-stone wall in an oak-birch wood. In addition, it was found on mosses on epidiorite at an altitude of 1000 m in the Ben Alder range of Inverness-shire by Dr O. L. Gilbert; the specimen is sterile but has pycnidia with the characteristic macroconidia. In Britain *M. cinerea* usually occurs at lower altitudes (mostly below 300 m), and exhibits a distribution pattern attributable to the General Western Group of Coppins (1976). However, there are two outlying easterly localities (in North Northumberland and East Perth) both of which are sheltered, more or less undisturbed, valley woodlands.

From outside Britain I have seen material of *M. cinerea* from Hordaland and Rogaland in western Norway, the east Sudety and Vysoké Tatry of Czechoslovakia, southern Germany, and the Swiss, Austrian and Italian Alps. Most collections from southern Germany and the Alps are



Map 6 *Micarea cinerea* ● 1950 onwards ○ Before 1950

from the trunks of conifers (*Picea, Pinus,* and *Abies*), but they also included specimens from the trunks of *Alnus* and *Betula,* lignum of stumps, fallen trees, and old fence posts. In addition, it was collected several times on thin twigs of *Picea* by F. Arnold and his contemporaries, and it is possibly of interest to note that I do not know it as an inhabitant of twigs in north-west Europe.

Unlike *M. alabastrites* and *M. peliocarpa, M. cinerea* is not known from Macaronesia, and I have not seen any material of it from outside Europe.

Exsiccata: Arnold *Lich. Exs.* 548 (M), 549 (BM ex K, M). Arnold *Lich. Mon.* 47 (BM ex K), 115 (BM ex K, M, MANCH), 116 (BM ex K, M). Britz. *Lich. Exs.* 846 (M). Hepp *Flecht. Eur.* 21 *p.p.* (BM, M). Lojka *Lich. Hung.* 60 (M). Vězda *Lich. Sel.* 1087 (BM, S). Zwackh *Lich. Exs.* 898 (M).

8. **Micarea contexta** Hedl.
(Figs 12A, 40A–B)

in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 83, 96 (1892). – *Catillaria contexta* (Hedl.) Zahlbr, *Cat. lich. univ.* **4**: 35 (1926). Type: Sweden, Hälsingland, Ovanåker, 1891, *J. T. Hedlund* (S – lectotype!).

Thallus effuse, endoxylic, inapparent or evident as a slight bleaching of the wood, consisting of scattered, small, rounded granules (*c.* 15–25 μm diam) buried between the wood fibres; external hyphae of granules with dark green walls, K−, HNO_3+ red. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia numerous, immarginate, ± globose from the start, often becoming tuberculate, black, matt, 0·1–0·2 mm diam, or to 0·3 mm diam when tuberculate. *Hymenium* 35–45 μm tall; upper part (epithecium) dark green, K− or green intensifying, HNO_3+ purple-red; remaining (lower) part ± hyaline or dilute greenish with dark green, vertical streaks, sometimes with a few, minute, purple-violet (K+ aeruginose) granules. *Asci* clavate, 35–40×10–14 μm. *Spores* ovoid or oblong-ovoid, upper cell broader than the lower and with a more rounded apex, 1-septate, or rarely with a thin, additional septum in the lower cell, 7–13(–14)×(2·3–)3–4·5 μm. *Paraphyses* rather scanty, of two types: *p. max. p.* branched and anastomosing, haline, thin, 0·6–0·8 μm wide, apices often with thickened, pigmented walls and then to 2 μm wide; *p. min. p.* scattered or in small fascicles, simple, with thickened, pigmented walls throughout and 1·5–2 μm wide, apices sometimes widening to 3 μm. Many apices overtopping the asci to form a ± distinct epithecium. *Hypothecium* 20–90 μm tall, dark green or dark purple (colours often intermixed), K+ dark olive-green or aeruginose, HNO_3+ purple-red; hyphae interwoven, hyaline or thickened with pigment, 1–2 μm wide; ascogenous hyphae with swollen cells to 4 μm wide. *Excipulum* indistinct, sometimes evident as a narrow, dark greenish zone, *c.* 5–12 μm wide, forming a lateral border to the reflexed edge of the hymenium.

Pycnidia usually present but inconspicuous, immersed between the wood fibres or emergent to sessile, black, with dark greenish walls, K – or green intensifying, HNO_3+ purple-red; of two types (a) *c.* 40 μm diam; *conidia* (*mesoconidia*) cylindrical, often faintly biguttulate 3·8–4·7×1·3–1·8 μm; (b) *c.* 20–40 μm diam; *conidia* (*microconidia*) narrowly cylindrical, 4–5× 0·8–1 μm.

Chemistry: Apothecia sections C−; material insufficient for analysis by t.l.c.

Observations: Micarea contexta is characterised by its endoxylic thallus, very small, black, ± globose apothecia, dark green epithecium, dark greenish or purplish hypothecium, ovoid, 1-septate spores, thin hyaline paraphyses and an absence of stalked pycnidia. It is apt to be confused with diminutive, immature forms of *M. melaena*, but that species has more numerous paraphyses, longer microconidia, and a superficial, granular thallus which contains gyrophoric acid when in a healthy condition. When mature, *M. melaena* has more robust apothecia and larger, 3-septate spores. *M. eximia* can be distinguished from *M. contexta* by its more brightly coloured epithecium and narrower, ± fusiform spores; and *M. nigella* can be distinguished by its simple spores and stalked pycnidia. *M. olivacea* differs in having more numerous paraphyses which are broader (1–1·2 μm) when hyaline, a complete absence of purple pigmentation in its apothecia, and relatively narrower, ± oblong spores.

Habitat and distribution: M. contexta occurs on conifer lignum, probably in sheltered, woodland situations. Species associated with *M. contexta* on the specimens examined include *Arthonia helvola, Cetraria pinastri, Cladonia* spp., (scattered squamules), *Hypogymnia physodes, Lecanora symmicta* agg., *Lecidea efflorescens, L. pullata, Micarea anterior, M. misella, Parmeliopsis ambigua,* and *P. hyperopta*.

The known distribution of *M. contexta* is restricted to middle Sweden, from where it was found in several localities by Hedlund. Supposed collections from outside Sweden seen by me belong to *M. melaena*. Nevertheless, *M. contexta* should be sought for in other regions, especially those containing naturally occurring coniferous forests.

Exsiccata: Malme *Lich. Suec.* 28 (M, S).

9. **Micarea crassipes** (Th. Fr.) Coppins, **comb. nov.**
(Figs 4B, 12B, 41C)

Helocarpon crassipes Th. Fr., *Lich. arctoi*: 178 (1860); and in *Nova Acta R. Soc. Scient. Upsal.* III, **3**: 278 (1861). – *Lecidea crassipes* (Th. Fr.) Nyl. in *Flora, Jena* **45**: 464 (1861). Type: Norway, Finnmark, Aldjok, 1857, *Th. M. Fries* (S – lectotype!; isolectotypes: BM!, BM ex K!, LD, UPS!).

Lecidea crassipes f. *moriformis* Th. Fr., *Lich. Scand.* **2**: 520 (1874). Type: Norway, Finnmark, Måsöy, 16 vii 1864, *Th. M. Fries* (UPS – lectotype!).

Lecidea crassipes f. *pulverula* Th. Fr., *Lich Scand.* **2**: 520 (1874). Type: Norway, Sör-Tröndelag, Oppdal hd., Dovre, Kongsvoll, Högsnyta, 11 viii 1863, *Th. M. Fries* (UPS – lectotype!).

Lecidea hypopodia f. *subassimilata* Nyl. in *Bull. Soc. linn. Normandie,* IV, **1**: 242 (1887). Type: U.S.A., Alaska, Bering Strait, St Lawrence Island, 1879, *E. Almquist* (H-NYL 20915 – holotype!).

Thallus growing on bryophytes or plant debris, rarely spreading on to sandy soil, composed of small, ± globose areolae. Areolae cream-white, pale grey-brown, sometimes ash-grey in part, matt, rather fragile, 0·07–0·2 mm diam; the larger areolae sometimes budding to produce smaller, secondary granules thereby giving the thallus an isidiose appearance. Areolae in section without a hyaline covering layer; thallus hyphae entirely hyaline, *c.* 2–3 μm wide. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia numerous, sessile but (in section) markedly constricted below, or turbinate, or short-stalked, 0·2–0·6 mm diam; disc matt, at first plane with a thin, often slightly raised, concolorous or slightly paler, often ± glossy, margin, 0·02–0·05 mm wide; disc later expanding, becoming convex and excluding the margin. On rare occasions apothecia become tuberculate and up to 1·4 μm diam. *Hymenium* 45–50 μm tall; upper part (epithecium) dark green or olivaceous and K+ green-intensifying, or purple-brown and K+ purple-intensifying; remaining (lower) part dilute purplish, K+ purple-intensifying or K+ sordid-green. *Asci* clavate, 40–48×11–14 μm. *Spores* 0(–1)-septate, fusiform-ellipsoid, (9–)10–17(–21)×(2·5–)3–4·5 μm. *Paraphyses* numerous, simple, or sparingly branched above, sometimes anastomosing, 1–1·5 μm wide, sometimes widening above to 2·5 μm; apical walls hyaline but often surrounded by dense pigment. *Hypothecium* dark, variably pigmented: upper part (*c.* 30–60 μm) dark purple-brown, K+ dark olive-green, or K+ purple-intensifying in part or in whole; lower part (including 'stipe') paler and mottled, brown- or vinose-red and K−, or with purple tinge and K+ purple-intensifying; hyphae in upper part tightly interwoven but becoming vertically orientated towards the hymenium, *c.* 1·5–2 μm wide, embedded in a densely pigmented gel-matrix, intermixed with ascogenous hyphae *c.* 2·5–4 μm wide; hyphae in lower part loosely interwoven, becoming outwardly directed laterally (i.e. as they approach the excipulum), *c.* 1–1·5 μm wide, embedded in a gel-matrix that swells and partially dissolves in K. *Excipulum* well developed, and conspicuous in young mature apothecia, *c.* 50 μm wide laterally; innerpart concolorous with upper hypothecium; outer part dilute to dark olivaceous, K+ green-intensifying; hyphae radiating, branched and anastomosing, *c.* 1–1·5 μm wide. Excipular and hypothecial tissues usually extended vertically downwards to form a 'stipe' (Fig. 4B).

Pycnidia rare, sessile, black, *c.* 60–150 μm diam, ostiole sometimes gaping; walls *c.* 10–17 μm wide, green-black (K− or K+ green-intensifying) in upper parts, changing to dark red-brown (K−) below; *conidiogenous cells* elongate-ampulliform, strongly tapered towards the neck, 6–9×3–4 μm, neck 1–1·3 μm wide; *conidia* (? *mesoconidia*) cylindrical, 4·5–5·7×1·2–1·5 μm.

Chemistry: Thallus K−, C−, KC−, PD−; t.l.c.: no substances.

Observations: The combination of a finely granular (sometimes isidiose) whitish to grey, muscicolous thallus and turbinate or short-stalked, marginate (when young), black apothecia make this an easy species to recognise, even with a hand lens. Internally, the apothecia have a well differentiated excipulum and a distinctly two-zoned hypothecium. This structure, which is rather 'advanced' for a *Micarea*, has led me to deliberate on the merits of the monotypic genus *Helocarpon* Th. Fr. However, characters such as the basic arrangement, organisation and form of apothecial hyphae (including paraphyses), ascus structure, morphology of pycnidia, and thallus structure (including phycobiont), are still those of a *Micarea*. The vertical extension of excipular and hypothecial tissues to produce a 'stipe' is not unique to *M. crassipes*, and is found in some specimens of *M. lignaria* and *M. ternaria*, and in an undescribed species from New Zealand (North Island: Trounson Kauri Reserve, on hepatics on rotten stumps 1967, *D. M. Henderson* (E)). This last species closely resembles *M. crassipes* (e.g. apothecia marginate when young, apothecial pigmentation, thallus type) but has broader, ellipsoid or ovoid, 1-septate spores (13–16·5×5·5–7 μm) and rather sparse paraphyses.

Overall considerations of morphology and ecology lead me to assign *M. crassipes* to the group including *M. assimilata*, and it is to the account of that species the reader is referred for further discussions.

Habitat and distribution: M. crassipes grows over bryophytes and plant debris on the ground and amongst rocks in northern Fennoscandia and at high altitudes (probably above 1000 m) in the Alps and other central European mountains. From Norway and Sweden I have seen several collections from north of *c.* 63°N and in Russia it occurs on the Kola Peninsula. In Finland it extends to the southernmost parts (Karelia australis, *c.* 60°30′N). In central Europe it occurs in the western Sudety (Krkonoše, at 1000 m) of Czechoslavakia, and southwards its range extends east to the Alps (Austrian Tirol, and Dolomiti in north Italy) and west to the Transylvanian Alps (Munţii Retezat, at *c.* 2000–2500 m) of Romania. From outside Europe it has been collected on St Lawrence Island in the Bering Strait; it is quite likely to have a circumpolar distribution.

Exsiccata: Arnold *Lich. Exs.* 556 [A] (BM ex K, H, H-NYL 16578), 556B (BM ex K, H, H-NYL p.m. 5105), 1121 (BM ex K). Fellman *Lich. Arct.* 165 (BM ex K, H, H-NYL 16570). Malme *Lich. Suec.* 362 (BM). Norrlin and Nyl. Herb. *Lich. Fenn.* 194A, B(H). Vězda *Lich. Bohem.* 282(LD). Vězda *Lich. Sel.* 11 (BM).

10. **Micarea curvata** Coppins, **sp. nov.**

(Fig. 12C)

Thallus probabiliter albido-griseus vel brunneo-griseus, granuloso-verruculosus. *Algae* cellulis 4–7 μm diam. *Apothecia* immarginata, convexo-hemisphaerica mox tuberculata, atrobrunnea, 0·2–0·5 mm diam, aut ad 0·65 diam ubi tuberculata. *Hymenium c.* 60 μm altum, ± hyalinum, cum vittis verticalibus, pallide fuscis; parte summa (epithecio) pallide fuscis, K−, *Ascosporae* fabiformes vel valde curvatae, (0–)1-septatae, 9–11·7×2·5–3·8 μm. *Paraphyses* ramosae et anastomosantes, graciles, *c.* 0·8–1 μm latae, apicibus haud incrassatis et haud pigmentiferis. *Hypothecium* pallidum. *Excipulum* reflexum, pallidum, margine externo pallide fusescenti. *Pycnidia* ignota. *Thallus* et *apothecia* in sectione C+ rubra.

Typus: Germania, Guestphalia, Gravenhorst, in muro lapideo ad lapidem arenarium, leg. *Th. R. J. Nitschke* (WRSL –holotype!).

Thallus probably grey or brownish grey and granular-verrucose, but difficult to interpret in the single specimen in which the thallus is invaded by foreign algae and dematiaceous hyphae. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia convex-hemispherical to tuberculate, immarginate, dark brown, 0·2–0·5 mm diam, or to 0·65 mm diam when tuberculate. *Hymenium c.* 60 μm tall ± hyaline with pale fuscous brown vertical streaks; upper part (epithecium) pale fuscous brown, K−, HNO_3. *Asci* clavate, *c.* 45–50×10–13 μm. *Spores* fabiform or distinctly curved, (0–)1-septate, 9–11·7×2·5–3·8 μm.

Paraphyses branched and anastomosing *c.* 0·8–1 μm wide, not swollen or pigmented at apices. *Hypothecium* pale, tinged dilute straw-brown. *Excipulum* soon reflexed, internally pale with straw-brown tinge, becoming slightly darker (pale fuscous) towards the outer edge; hyphae radiating, branched and anastomosing, *c.* 0·8–1 μm wide.

Pycnidia not found.

Chemistry: Sections of thallus C+ red, PD−; sections of apothecia C+ red; probably containing gyrophoric acid but material insufficient for analysis by t.l.c.

Observations: M. curvata is characterised by its distinctly curved, 1-septate spores, fuscous brown pigment in the apothecia which is unchanged by K or HNO_3, and C+ red reactions (? gyrophoric acid) of apothecia and thallus in sections. It is reminiscent of *M. subnigrata* but that species has uncurved, ellipsoid spores and all parts C−. In outward appearance *M. curvata* is similar to some forms of the almost ubiquitous *Scoliciosporum umbrinum,* with which it could be mistaken in the field.

Habitat and distribution: M. curvata is known only from a single collection on sandstone in the Wroclaw Herbarium, which is labelled '*?Biatora nov. sp.* Auf einer Steinmauer bei Gravenhorst/Westfalen leg. Nitschke' (label kindly transliterated by Prof. Hertel). No recognisable associate species are present on the small specimen although there are a few, rounded, white areolae (C+ red) probably belonging to *Trapelia coarctata s. ampl.* From the appearance of the specimen it occurred in a humid, sheltered, possibly shaded or north-facing situation.

11. **Micarea denigrata** (Fr.) Hedl.

(Figs 1B, 13, 42; Map 7)

in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 78, 89 (1892). – *Biatora denigrata* Fr. in *K. svenska VetenskAkad. Handl.* **1822**: 265 (1822). – *Catillaria denigrata* (Fr.) Boistel, *Nouv. Fl. Lich.* **2**: 199 (1903). Type: Sweden, Småland, 'Femsjö in parietibus vetustus', *E. M. Fries* (UPS – lectotype! [t.l.c.: gyrophoric acid]).

Lecidea anomala f. *pyrenothizans* Nyl., *Lich. Scand.*: 203 (1861). – *Micarea denigrata* f. *pyrenothizans* (Nyl.) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 78, 89 (1892). Type: Finland, Nylandia, Helsingfors [Helsinki], on lignum, 1860, *W. Nylander* (H-NYL 21665 – lectotype!).

Lecidea parissima Nyl. *in* Crombie in *J. Bot., Lond.* **9**: 178 (1871), and in *J. Linn. Soc. Bot.* **11**: 484 (1871). Type: England, Middlesex, Hendon, on old pales, 1870, *J. M. Crombie* (H-NYL 21659 – holotype!; isotypes: BM!, BM ex K!).

Lecidea spodiza Nyl. in *Flora, Jena* **57**: 9 (1874). Type: Scotland, Perthshire, near Killin, on old worked conifer lignum, 1873, *J. M. Crombie* (H-NYL 21734 – lectotype!; BM – isolectotypes!).

Lecidea hemipoliella Nyl. in *Flora, Jena* **58**: 11 (1875). – *Micarea hemipoliella* (Nyl.) Vězda *in* Vězda & V. Wirth in *Folia geobot. phytotax., Praha* **11**: 100 (1976). – *Micarea denigrata* f. *hemipoliella* (Nyl.) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3) 78, 89 (1892). Type: Finland, Tavastia australis, Evo, ± smooth bark of *Alnus*, 1873, *J. P. Norrlin* (H – lectotype!, isolectotypes: H(×3)!, H-NYL 21691!).

Lecidea discretula Nyl. in *Flora, Jena* **58**: 444 (1875). Type: Romania, 'Circa Thermas Herculis in Banatu (Hung.), supra Daedaleam in trunco quercino', 1874, *H. Lojka* (H-NYL 21693 – holotype!).

Lecidea aniptiza Stirton in *Rep. Trans. Glasgow Fld Nat.* **4**: 85 (1876). Type: Scotland, Perthshire, Killiecrankie, on lignum, 1875, *J. Stirton* (GLAM – lectotype!; BM – isolectotype!).

Lecidea denigrata var. *submisella* Nyl. *in* Vainio in *Medd. Soc. Fauna Fl. fenn.* **3**: 112 (1878). – *Catillaria synothea* f. *submisella* (Nyl.) Blomb. & Forss., *Enum. Pl. Scand.*: 92 (1880). Type: Finland, Tavastia australis, Korpilahti, on lignum, 1874, *E. A. Lang* [Vainio] (H-NYL 21661 – lectotype!).

Lecidea spodiza f. *ecrustacea* Lamy in *Bull. Soc. bot. Fr.* **25**: 440 (1878). Type: France, Puy-de-Dôme, Monte Dore, near Cascade du Queureilh, on lignum of conifer trunk, 31 vii 1878, *Lamy* (H-NYL 21731 – lectotype!).

Lecidea praeviridans Nyl., *Suppl. Lich. env. Paris*: 5 (1879). – *Biatorina praeviridans* (Nyl.) Boistel, *Nouv. Fl. Lich.* **2**: 194 (1903). – *Catillaria praeviridans* (Nyl.) Zahlbr., *Cat. Lich. univ.* **4**: 64 (1926). Type: France, Haute Loire, Saugues, on *Pinus* bark, 18 –, *A. Boistel* (H-NYL 19221 – lectotype! [t.l.c.: gyrophoric acid]; BM – isolectotype!).

Lecidea denigrata f. *sublivescens* Nyl. in *Flora, Jena* **64**: 539 (1881). Type: Romania, Maramures, 'prope balneum kabola Pojána, com. Marmaros in Hung.', on bark of *Pinus sylvestris, H. Lojka* 4455, 'Lich. Hung. exs. (ined.) n. 305. ad int.' (H-NYL 11663 – holotype!).

Lecidea denigrata f. *pseudoglomerella* Harm. in *Bull. Séanc. Soc. Sci. Nancy*. II, **33**: 58 (1899 ['1898']). – *Catillaria denigrata* var. *pseudoglomerella* (Harm.) Boistel, *Nouv. Fl. Lich.* **2**: 199 (1903). Type: France, Meurthe-et-Moselle, La Malgrange, on oak posts [lignum], 8 v 1894, *J. Harmand*, Lich, Loth. 838*p.p.* (ANGUC – lectotype! [t.l.c.: gyrophoric acid]; DUKE – isolectotype!).

Catillaria prasina f. *longior* Erichsen in *Schr. naturw. Ver. Schleswig-Holst.* **22**: 101 (1937). Type: West Germany, Schleswig-Holstein, Lauenberg, Sachsenwald, Rev. Kl. Viert, on roots of old *Fagus,* 2 xii 1934, *C. F. E. Erichsen* (HBG – holotype!).

Micarea denigrata var. *friesiana* Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 78, 89 (1892); *nom. inval.* (Art. 26).

Micarea denigrata var. *friesiana* f. *vulgaris* Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 79, 90 (1892); *nom. inval.* (Art. 26).

Micarea andesitica Vězda *in* Poelt & Vězda, *Bestimmungsschl. europ. Flechten. Erganzungsheft* I: 160 (1977); *nom. nudum* (Art. 32). Spec. orig.: Hungary, Matra, Matrafüred, Pipis-Legy, 380 m, on andesitic rock, 17 xi 1976, *A. Kiszely & A. Vězda* (hb Vězda!).

?Lecidea hemipoliella semialbula* Stirton in *Rep. Trans. Glasgow Fld Nats.* **4**: 89 (1876). – *Biatorina synothea* var. *semialbula* (Stirton) A. L. Sm., *Monogr. Br. Lich.* **2**: 122 (1911). Type: Scotland, Sutherland, Altnaharra, on lignum, *Stirton* (not seen; not traced in BM or GLAM).

?Catillaria synothea f. *major* B. de Lesd., *Rech. Lich. Dunkerque,* Suppl. 1: 118 (1914). Type: France, Nord, Dunkerque, Ghyvelde, on piece of wood (*Pinus*) on the sand in a dune, *B. de Lesdain* (not seen).

?Catillaria synothea f. *fusca* B. de Lesd., *Rech. Lich. Dunkerque,* Suppl. 1: 118 (1914). Type: France, Nord, Dunkerque, St-Pol, on a stake, *B. de Lesdain* (not seen).

Lecidea synothea auct., non Ach. (1808). See note below.

Note: Lecidea synothea Ach. in *K. svenska VetenskAkad. Handl.* 1808: 236 (1808). From the comments on Acharian specimens by Hedlund (1892: 91) and my examination of Acharian material in BM, it is clear that this name was based on material of the common and widely distributed species generally known as *Bacidia umbrina* (Ach.) Bausch or *Scoliciosporum umbrinum* (Ach.) Arnold (basionym: *Lecidea umbrina* Ach, *Lich. Univ.*: 183 (1819)). In the 19th century '*synothea*' was commonly applied to *Micarea denigrata.* Despite Hedlund's comments, this misapplication has been continued by some authors, even in recent years (e.g. Ozenda & Clauzade, 1970: 402). To avoid the confusion that would arise if '*umbrina*' were replaced by '*synothea*', a formal proposal to reject the name *Lecidea synothea* Ach. (and combinations from that name), under the provision of Art. 69.1, will be presented elsewhere.

Thallus effuse and often widespreading, sometimes endoxylic but usually developing on the surface of the substratum (especially in the vicinity of apothecia) as convex to irregularly subglobose areolae. Areolae 60–200 μm diam, greenish white to greenish grey, matt; in section without an amorphous covering layer, external hyphae hyaline but surrounding gel matrix often with dilute olivaceous, K+ violet pigment. Thallus sometimes scurfy and dark grey-brown to blackish, owing to invasion by dematiaceous fungi and non-lichenized algae. *Phycobiont* micareoid, cells *c.* 4–7 μm diam.

Apothecia usually present and numerous (see 'observations' below), scattered to confluent, broadly convex to subglobose, sometimes tuberculate, 0·15–0·5 mm diam, or to 0·6 mm when tuberculate; immarginate, or sometimes young apothecia with an indistinct, shallow marginal rim, paler than the disc; disc pallid to brown or piebald (shade forms), more usually dark grey or black, matt. *Hymenium* (25–)30–40 μm tall, dilute olivaceous or dull brownish, K+ violet; pigment often concentrated in upper part (with lower part ± hyaline), and confined to the gel-matrix. *Asci* clavate, 28–36×9–12 μm. *Spores* oblong-ellisoid, oblong-ovoid, fusiform or bacilliform, often slightly curved, (0–)1-septate, upper cell usually slightly shorter and broader than the lower, (7–)9–16(–18)×2–3·3(–3·5) μm. *Paraphyses* numerous, branched and sometimes anastomosing, 1–1·5(–1·7) μm wide; apices scarcely wider, and never with closely adhering pigment. *Hypothecium* 60–110 μm tall, hyaline or very dilute yellowish straw; hyphae *c.* 1–1·5 μm wide, interwoven or some vertically orientated in upper part, intermixed with short-celled, ascogenous hyphae hyphae *c.* 2–4 μm wide. *Excipulum* indistinct, but usually evident in sections of young, shallow-convex apothecia, hyaline; hyphae radiating, branched and anastomosing, hyaline, *c.* 1–1·5 μm wide.

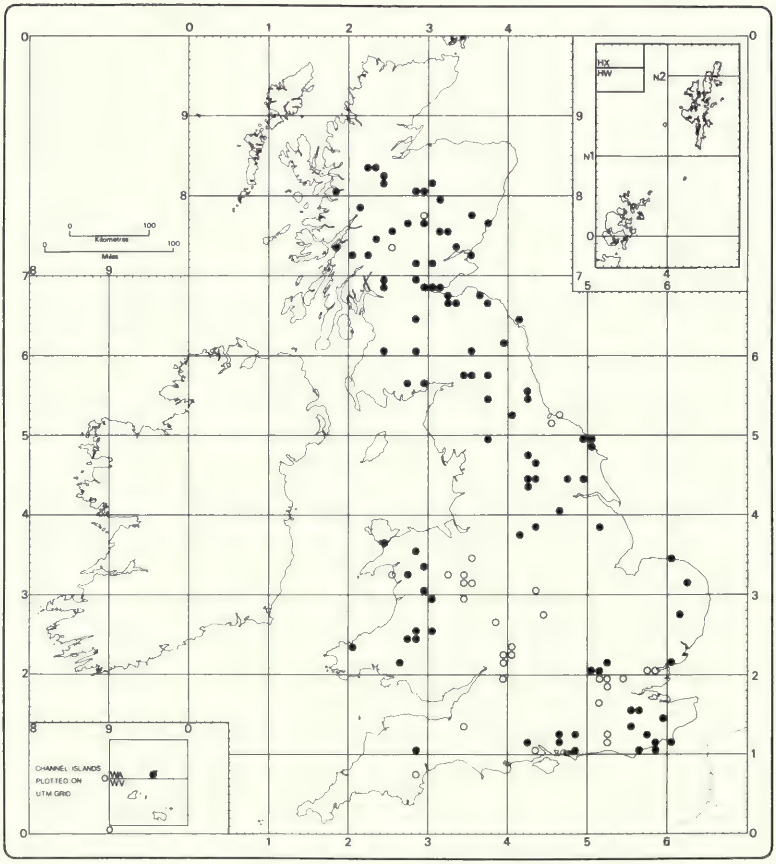
Pycnidia usually present and numerous, immersed in the thallus or substratum (endoxylic forms), sometimes emergent, hyaline grey or black; walls hyaline but usually dilute olivaceous or brownish, and K+ violet in the upper (exposed) parts; in endoxylic forms, walls olivaceous (K+ violet) throughout; of three types: (a) 60–150 μm diam, ostioles eventually gaping; *conidia* (*macroconidia*), curved or hamate, (1–)3-septate, 12–24×*c.* 1 μm; (b) 80–160 μm diam, ostioles often gaping: *conidia* (*mesoconidia*) short cylindric or obovate, sometimes faintly biguttulate, 2·8–4·5(–5)×1·2–1·8 μm often extruding from the ostioles as a conspicuous white blobs; (c) 30–50 μm, ostioles not gaping; *conidia* (*microconidia*) narrowly fusiform or bacilliform, (4·5)5–7·5×0·7–0·8 μm.

Chemistry: Thallus K−, PD−; sections of thallus and apothecia C+ orange-red, rarely C− (also, parts with dull olivaceous pigment, C+ violet). If thallus is heavily parasitised and scurfy the C+ orange-red reaction may be difficult to obtain and gyrophoric acid may not be detectable by t.l.c.

Observations: Micarea denigrata is a common and extremely polymorphic species exhibiting a wide range of genotypic and phenotypic variation. Its thallus can vary from being completely endoxylic to forming a thick, granular-verrucose, areolate crust. The colour of the apothecia varies from pallid, through grey or brown, to black in a ± direct relationship with exposure to light. Specimens may be abundantly fertile with numerous, large, mature apothecia. On the other hand, they may be ± sterile with just a few, scattered immature apothecia (or even none at all) but with numerous pycnidia containing mesoconidia; alternatively the latter may be replaced by pycnidia containing microconidia and, or, macroconidia. Indeed, all possible combinations of anamorphic states have been found and a few collections (e.g. *Coppins* 1888 and 8384) have all three states, plus apothecia, on the same thallus. Spore length is usually in the range of 9–14 μm, but extreme forms are known in which the range is 8–10 μm, or 12–18 μm. Gyrophoric acid is usually present in the thallus and/or the apothecia (and easily demonstrated by tests with C), but in some specimens its concentration is low and only detectable with certainty by t.l.c.; in a few diminutive, endoxylic forms I have been unable to detect gyrophoric either by a C test, or by t.l.c. In short, *M. denigrata* exhibits extreme variation. Despite this, with care and patience the species is rarely difficult to separate from other, similar species. The biggest problems I have experienced are where the decision has to be made between what could be a diminutive form of *M. denigrata* with small spores, or a form of *M. misella* with an unusually high proportion of 1-septate spores and without its characteristic stalked pycnidia (that contain mesoconidia). Such decisions are settled by the careful observation and measurement of paraphyses, and microconidia (see couplet 11 of the main key and Table 7). Shade forms of *M. denigrata* with brown, ± globose apothecia have been confused with *M. elachista*, but the latter has a brown (K+ dissolving) epithecial pigment, a more complex thallus structure (with a 'cortex' and amorphous covering layer), distinctive pycnidia, and always lacks gyrophoric acid (sections of thallus and apothecia C−). Forms of *M. denigrata* with a scurfy-granular thallus can be similar to *M. prasina*, but microscopic examination will show the thallus appearance to be caused by its disruption by invading foreign fungi and algae, and not by the presence of the small ± discrete granules (goniocysts) characteristic of *M. prasina.* Furthermore, *M. prasina* never gives C+ orange-red (gyrophoric acid) reactions, and it usually has broader, rarely curved spores with more rounded apices. The closest relative to *M. denigrata* is *M. nitschkeana*, which is ± identical with regard to thallus structure, pycnidial types, apothecia structure, pigmentation, and chemistry. Morphologically the only important difference is that the mature spores of *M. nitschkeana* are 3-septate and more consistently curved (cf. Figs 13 and 24B). In addition, the two species differ in their preferance of substrata: *M. denigrata* favouring lignum or dead bark of old tree trunks or stumps, and *M. nitschkeana* favouring corticate twigs and small branches of trees and shrubs. However, there is some degree of overlap as *M. nitschkeana* is occasionally found on the lignum of fence posts, but, on the other hand, I have never encountered *M. denigrata* on attached living, corticate twigs. In the field, well developed specimens of *M. denigrata* sometimes have a superficial resemblance to *M. cinerea, M. lignaria,* and *M. peliocarpa*, but these three species have K− hymenia and larger, 3 (or more)-septate spores. Diminutive endoxylic forms of *M. denigrata* are indistinguishable in the field from the several, predominantly lignicolous species with small, black apothecia, but all such species (except *M. misella* as discussed above) appear very different when examined microscopically.

Habitat and distribution: M. denigrata is commonly found on the lignum of fallen trunks and old stumps of broad-leaved and coniferous trees, especially in rather open situations at the edges of woodlands, woodland glades, and hedgerows, etc. The communities in which it occurs are difficult to define, but to give some indication the following list of associated species has been made from collections from fallen decorticate trunks of *Pinus* in the native pine-woods of Scotland: *Buellia griseovirens, Cladonia coniocraea, C. macilenta, Hypogymnia physodes, Lecanora expallens, L. symmicta* agg., *Lecidea aeruginosa, L. icmalea, Micarea peliocarpa, Mycoblastus sterilis, Parmelia saxatilis, Platismatia glauca, Pseudevernia furfuracea, Xylographa abietina,* and *X. vitiligo.*

M. denigrata is a very successful primary coloniser of untreated timber-work. It also occurs on the same substrate whose preservative has lost its effectiveness, or whose painted surface has flaked off. On such substrata *M. denigrata* has been found in a wide range of situations, e.g. gates, fence posts and rails, garden furniture, picnic tables and seats, window frames of greenhouses, wooden roof tiles (shingles), telegraph poles, and the woodwork of old carts and farm machinery. When on such worked wood it often forms almost pure stands, and is often present as a form with few apothecia but numerous pycnidia containing mesoconidia; the conidia often extruding as white blobs easily visible to the unaided eye or through a ×10 lens. Lichens associated with *M. denigrata* on worked wood in the British Isles include *Buellia punctata, Cyphelium inquinans, Hypogymnia physodes, H. tubulosa, Lecanora conizaeoides, L.*



Map 7 *Micarea denigrata* ● 1950 onwards ○ Before 1950

dispersa agg., *L. piniperda*, *L. pulicaris*, *L. saligna*, *L. symmicta* agg., *L. varia*, *Lecidea aeruginosa*, *L. icmalea*, *Mycoblastus sterilis*, *Parmelia sulcata*, *Scoliciosporum chlorococcum*, *S. umbrinum*, *Strangospora moriformis*, and *Thelocarpon laureri*.

Further evidence of the pioneering abilities of *M. denigrata* comes from the find (Coppins 1888) of it on hardboard lying in a dune-slack, and the observations by Poelt (1977; as *M. hemipoliella*) on its colonisation of dead leaves of *Cladium mariscus* in a fen in Bavaria. Other reports on soft vegetable matter are wanting, although I have found it on decaying mosses (with *Cladonia chlorophaea* agg.) on the slope of a stable sand dune on Holy Island in Northumberland (*Coppins* 4456).

M. denigrata is occasionally found on the rather dry and loose bark of old trees (e.g. *Acer pseudoplatanus*, *Alnus*, *Betula*, *Castanea*, *Sambucus*, *Ulmus*, and *Pinus*), usually towards their bases; however occurrences on ± smooth bark are very rare (e.g. type material of *Lecidea hemipoliella*, on *Alnus* in southern Finland). To my knowledge *M. denigrata* never occurs on the healthy, living twigs of trees, or shrubs (see 'observations' above). There are two British collections on shaded sandstone, one from Fife in a conifer plantation, the other from Yorkshire in a ditch embankment; associated species included *Lecidea granulosa* agg., *L. icmalea*, *Micarea peliocarpa*, and *Parmeliopsis ambigua*. In addition, it has been found growing with *Psilolechia lucida* on the east-facing vertical side of a tomb in a Suffolk churchyard.

M. denigrata is widely distributed in mainland Britain, but has not yet been reported from Ireland. In mainland Europe it is again widespread although I have not seen material from north of about 67°N; its range extends into eastern Europe and the Balkans and continues to the Caucasus. I have examined North American material from Newfoundland, Washington (state), and Colorado, thus suggesting a widespread distribution in that subcontinent.

Exsiccata: Anzi *Lich. Ital.* 256 (BM). Arnold *Lich. Mon.* 46 (BM ex K). Britz. *Lich. Exs.*: 464 *p.p.* (H). Fries *Lich. Suec.* 98 (E, UPS). Harm. *Lich. Loth.* 838 (ANGUC, DUKE). Hepp *Flecht. Eur.* 14 (E). Johnson *Lich. Herb.* 373 (BM). *Krypt. Exs. Vindob.* 3153 (BM, BM ex K), 3651 (BM, BM ex K, M), 4858 (GZU). Kuták *Lich. Bohem.* 205 (O), 516 (O), 517 (O). Malbr. *Lich. Norm.* 387 (M). Malme *Lich. Suec.* 145 (M, S). Migula *Crypt. Germ.* 132 (BM, E, MANCH). Mougeot & Nestler *Stirpes Crypt.* 1329 *p. min. p.* (BM). Norrlin & Nyl. *Herb. Lich. Fenn.* 177 (BM, H), 745 (BM, H). Poelt *Lich. Alp.* 22 (BM, M, WIS). Rabenh. *Lich. Eur.* 626 (BM, BM ex K, E). Samp. *Lich. Port.* 132 (LD). Vězda *Lich. Sel.* 1430 (BM). Weber *Lich. Exs.* 73 (E, DUKE, M, NMW, WIS). Zwackh *Lich. Exs.* 394 (BM ex K, H).

12. **Micarea elachista** (Körber) Coppins & R. Sant., **comb. nov.**
(Figs 1C, 14A)

Biatora elachista Körber, *Parerga lich.*: 159 (1860). – *Catillaria elachista* (Körber) Vainio in *Acta Soc. Fauna Fl. fenn.* **57** (2): 455 (1934). Type: Germany, Baden-Württemberg, Heidelberg, on old trunk of *Castanea sativa*, *W. E. von Ahles* (L 910, 138–100–lectotype!; L 910, 138–32–isolectotype!) See note below.

Lecidea anomala **L. glomerella* Nyl., *Lich. Scand.*: 203 (1861). – *Biatorina glomerella* (Nyl.) Arnold in *Flora, Jena* **53**: 474 (1870). – *Catillaria glomerella* (Nyl.) Th. Fr., *Lich. Scand.* **2**: 578 (1874). – *Micarea glomerella* (Nyl.) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 75, 85 (1892). Type: Finland, Ostrobottnia australis, Botom, 1859, *A. J. Malmgren* (H-NYL 19123 – lectotype!).

Lecidea poliococca Nyl., *Lich. Scand.*: 203 (1861). – *Catillaria denigrata* f. *poliococca* Vainio in *Acta Soc. Fauna Fl. fenn.* **57** (2): 460 (1934). – *Catillaria synothea* var. *poliococca* (Nyl.) Erichsen in *Annls mycol.* **41**: 205 (1943). Type: Sweden, Uppland, 'Upsalia', in silva 'Parken', ad pinos decorticatos', 1852, *W. Nylander* (H-NYL 19144 – holotype!).

Lecidea sororians Nyl. in *Flora, Jena* **58**: 445 (1875). – *Bacidia sororians* (Nyl.) H. Olivier in *Bull. Géogr. bot.* **21**: 168 (1911). Type: Finland, Tavastia australis, Korpilahti, near Raianlahti, on rock with *Stigonema* sp., 1873, *E. A. Lang [Vainio]* (H-NYL 17234 – holotype!).

Lecidea glomerella f. *simplicata* Nyl. in Vainio in *Medd. Soc. Fauna Fl. fenn.* **10**: 28 (1883). Type: Finland, Tavastia australis, Evo, 'supra truncum pineum', 1874, *J. P. Norrlin*, Norrlin & Nyl. *Herb. Lich. Fenn.* 314 (H – lectotype!; isolectotypes: BM!, H! M!).

Lecidea glomerella var. *poliococcoides* Vainio in *Medd. Soc. Fauna Fl. fenn.* **10**: 29 (1883). Type: Finland, Karelia borealis, Lieksa, Vieki, on burnt lignum, 1875, *E. A. Vainio* (TUR-VAINIO 22326 – holotype!).

Catillaria elachista var. *carbonicola* Vainio in *Acta Soc. Fauna Fl. fenn.* **57** (2): 458 (1934). Type: Finland, Tavastia australis, Korpilahti, 'hiiltyneella kannolla', 1873, *E. A. Lang [Vainio]* (H-NYL 19143 – isotype!).

Notes on the typification of Biatora elachista *Körber*: In the protologue to *B. elachista,* Körber (loc. cit.) gives the following habitat and locality information: 'On alten Strünken der *Castanea vesca* bei Heidelberg von Hrn. v. Zwackh und Ahles aufgefunden.' Material borrowed from the Körber Herbarium (L) consisted of four specimens: i. bei Heidelberg, *Zwackh,* annotated: 'Biatora elachista Kbr. nov. sp.' (L 910, 138–101). ii. Heidelberg, *Ahles* (L 910, 138–100). iii. identical label as ii. (L 910, 138–32). iv. Forstrevier Goleow bei Rybnik, iii 1872, *B. Stein* (L 910, 138–298). (i–iii) are on *Castanea* lignum and (iv) is on conifer lignum.

The most obvious choice for lectotype is (i) but it is not a *Micarea* and does not conform to the usual interpretation of the name (e.g. Vainio, 1934: 45; Ozenda & Clauzade, 1970: 401). I do not know the identity of this species, but it may be close to *Lecidea hypopta* Ach.; a brief description follows:

> Thallus probably mostly endoxylic but obscured by a pale farinose crust of a non-lichenised alga. Apothecia numerous, reddish brown to brown-black, epruinose 0·15–0·3 mm diam. Young apothecia with a pale margin which is soon excluded as the disc expands and becomes convex. Epithecium reddish brown, turning olivaceous brown in K. Hymenium 30–35 μm tall. Paraphyses simple or forked in their upper part, *c.* 1–1·5 μm wide; upper 5–15 μm often with pigmented walls and up to 2·5 μm wide. Asci clavate 28–35×10–11 μm, 8-spored. Spores simple or 1-(rarely 2-) septate oblong-ellipsoid, straight or slightly curved, contents often becoming brown, 8–13×3–4 μm. Excipulum hyaline within, reddish brown at edge, often with a penetrating algal layer *c.* 25 μm wide. Algal cells *c.* 7–13 μm diam. Pycnidia not found.

Specimens (ii) and (iii) are presumably those that Körber attributed to Ahles in the protologue and are therefore syntypes. Both belong to the species generally known as *Catillaria elachista* (Körber) Vainio, and it is with these that the name is lectotypified here. Specimen (iv) is not a syntype and does not belong to either of the above taxa. It has small, brown thinly white-pruinose apothecia, a dark reddish brown hypothecium and small, ellipsoid spores, 7–8×2·5–3 μm, and is referable to *Lecidea apochroeella* Nyl.

Thallus effuse, superficial, consisting of dispersed to continuous, convex to subglobose areolae; areolae greenish white or whitish grey, sometimes tinged grey-brown or olivaceous, occasionally dark brown (when on burnt lignum), matt, sometimes ± white-pruinose, *c.* 0·08–0·16(–0·25) mm diam. Areole in section (Fig. 1C) with a *c.* 10–12 μm tall, hyaline or greyish (pigment in gel-matrix, K+ violet), algal-free 'cortex', composed of interwoven, hyaline hyphae (*c.* 1·5 μm wide) that separate in K; outer surface of cortex sometimes bound by a hyaline, amorphous, densely gelatinised layer ('epicortex'), *c.* 3–5 μm tall. This organised structure with a 'cortex' and 'epicortex' is often disrupted by the invading torulose hyphae of a dematiaceous hyphomycete. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia usually numerous, immarginate, convex to ± globose, often becoming tuberculate, dark brown to brown-black, matt, (0·08–)0·12–0·3 mm diam, or to 0·8 mm diam when tuberculate. *Hymenium* 30–40 μm tall. Upper part (epithecium) usually well defined, up to 12 μm tall, dark fuscous-brown; pigment concentrated into dense amorphous clumps, but dissolving and fading into solution (without changing colour) in K, HNO_3- and not dissolving; epithecium of young apothecia sometimes Kf+ violet due to the additional presence of the dull olivaceous, K+ violet pigment which occurs in greater concentrations in the pycnidia. Remaining (lower) part of hymenium, hyaline with dilute yellowish brown vertical streaks. *Asci* clavate, 23–35×10–12 μm. *Spores* fusiform, oblong-fusiform or ovoid-oblong, often slightly curved, mostly 0–1-septate and slightly constricted at the septum, (9–)11–15(–19)×2–3·5 μm; occasionally becoming 2- or 3-septate and up to 20–24 μm long; old spores sometimes with brownish contents. *Paraphyses* numerous, hyaline throughout, 0·8–1 μm wide in mid-hymenium but gradually widening above to 1·7(–2) μm; sparingly branched and sometimes anastomosing, but becoming richly branched above where their entangled apices, together with the brown pigment, form a ± well delimited epithecium. *Hypothecium* 60–150 μm tall, pale, tinged dilute yellowish brown, K−, HNO_3-; hyphae hyaline, 1–1·5 μm wide, interwoven, becoming ± vertically orientated towards the hymenium; ascogenous hyphae with swollen cells, mostly 2–

4 μm wide. *Excipulum* poorly developed and much reflexed, sometimes evident as a narrow, pale fuscous-brown zone; hyphae hyaline, radiating, branched and anastomosing, 1–1·5 μm wide.

Pycnidia usually present and numerous, developing from within areolae but soon becoming emergent and sometimes ± sessile; of two types: (a) *c.* 100–200 μm diam, grey-brown but usually paler or whitish around the ostiole, surface smooth and ± glossy; ostioles distinct and *c.* 20 μm diam, sometimes gaping and to 50 μm diam; wall not continuing below the base, laterally *c.* 23–40 μm wide, dilute olivaceous or brownish, K+ violet, and formed of interwoven hyaline hyphae (*c.* 1·5 μm wide) that ± separate in K; *conidiogenous cells* cylindrical, occasionally percurrently proliferating, *c.* 4–7×1–2 μm; *conidia* (*mesoconidia*) ± cylindrical, sometimes slightly wider at proximal end, often faintly biguttulate, 3·5–4·5×1·3–1·7(–2) μm. (b) similar in appearance and structure to above, but smaller and 60–100 μm diam; *conidiogenous cells* cylindrical, *c.* 3–6×1 μm; *conidia* (*microconidia*) narrowly cylindrical, (4–)4·5–6(–6·5)× 0·7–1 μm.

Chemistry: Thallus K−, C−, KC−, PD−; sections of apothecia C−; no substances detected by t.l.c.

Observations: The combination of ± globose areolae, ± globose, brown apothecia, dense brown (dissolving in K) epithecial pigment, C− hymenium, fusiform, 1–3-septate spores and distinctive, ± glossy pycnidia usually make this species easy to identify. Some confusion has been made with shade forms of *M. denigrata*, but these can be distinguished by their rather adnate and often larger apothecia, C+ orange-red (gyrophoric acid) hymenium and thallus, never glossy, thin-walled pycnidia, and, when present, curved macroconidia. *M. elachista* is closely related to *M. rhabdogena* (*q.v.*), which differs in having an endoxylic thallus, smaller, mostly simple, spores, and black pycnidia.

The areolae of *M. elachista* sometimes have a white-pruinose appearance: the 'pruina' resulting from the partial disintegration of the thin 'epicortex'.

Habitat and distribution: M. elachista is found, often in the company of *Parmeliopsis* spp., on the lignum (rarely bark) of partially or wholly decorticate trunks or large stumps of old trees, especially *Castanea, Pinus*, and *Quercus*. Most collections from France and Germany were made from *Castanea*, whereas those made from Scandinavia were mostly from conifers. It occasionally occurs on burnt or charred stumps and my collection (*Coppins* 6017) from Sweden, on *Pinus*, was accompanied by *Chaenotheca ferruginea, Hypocenomyce friesii, Lecidea granulosa* agg., *Micarea melaena*, and *Parmeliopsis* spp. It seems to be rare on worked timber, but was collected on old fence-posts in Bavaria by Arnold.

I have seen only one saxicolous gathering of *M. elachista*, i.e. the holotype of *Lecidea sororians* from southern Finland, with which occurred colonies of a *Stigonema* sp., a few lobes of a brown *Parmelia* (? *P. verruculifera*) and, according to Nylander, *Biatorella torvula* (not present in the existing material). This specimen is very small and in poor condition, and the few spores seen appeared to be abnormally developed, 1–3-septate, 15–24×2–2·5 μm; other features of the thallus and apothecia agree with *M. elachista* (pycnidia were not found) and I think it is most unlikely to represent a distinct taxon.

M. elachista appears to avoid the more strongly oceanic areas of Europe, and is known from mid-Sweden, southern Finland, France (Haute Vienne, the Massif Central and the Pyrénées), southern Germany (Hessen, Baden-Württemberg and Bavaria), and the Austrian Tirol. Its presence in Britain is a possibility and it should be sought for, especially in the central Highlands and east Scotland, and the Welsh border counties.

Exsiccata: Arnold *Lich. Exs.* 1471 (BM ex K, M). Arnold *Lich. Mon.* 246 (BM ex K, M). Malme *Lich. Suec.* 21 (M, S). Norrlin & Nyl. *Herb. Lich. Fenn.* 314 (BM, H, M); 724 (BM). Vězda *Lich. Sel.* 1134 (BM). Zwackh *Lich. Exs.* 122 (H-NYL 18828, M).

13. **Micarea eximia** Hedl.
(Figs 14B, 40C)

in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 80, 84, 95 (1892). – *Catillaria malmeana* Zahlbr., *Cat. lich. univ.* **4**: 56 (1926); *nom. nov.*; non *Catillaria eximia* Malme. Type: Sweden, Dalarna, Älvdal, Hållstugen, vi 1891, *J. T. Hedlund* (S – lectotype! [t.l.c.: no substances]; S – isolectotype!; material distributed as Malme *Lich. Suec. Exs.* 26 is possibly part of this collection).

Thallus effuse, endoxylic, of minute clusters (*c.* 15–40 μm diam) of the phycobiont amongst the wood fibres, with intertwining hyphae that often have green walls, K−, HNO_3+ red. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia numerous, immarginate, ± convex-globose from the start, often becoming tuberculate, black, matt or slightly glossy, 0·1–0·2 mm diam, or to 0·4 mm diam when tuberculate. *Hymenium* 30–45 μm tall; upper part bright to dark aeruginose, K− or dulling, HNO_3+ purple-red; remaining (lower) part ± hyaline with aeruginose vertical streaks. *Asci* clavate, *c.* 30–40×11–12 μm. *Spores* oblong-fusiform, sometimes slightly curved, 9–14 (–16)×1·8–2·5 μm. *Paraphyses* rather scanty, branched and anastomosing, thin and 0·7–0·8 μm wide, but upper *c.* 5–17 μm with thickened, pigmented walls and then 2–3 μm wide; usually a few paraphyses have pigmented walls throughout their length and are about 2 μm wide in the middle hymenium. *Hypothecium* 45–120 μm tall, dilute reddish- or purplish brown, sometimes with darker blotches, K+ dull greenish, HNO_3+ purple-red, pigment confined to gel-matrix; hyphae interwoven, hyaline, *c.* 1–1·5 μm wide; ascogenous hyphae with swollen cells up to 4 μm diam. *Excipulum* indistinct, sometimes evident as a dark green or brownish (K+ olivaceous) reflexed zone with branched, radiating, pigmented hyphae *c.* 1·5–2 μm wide.

Pycnidia numerous but inconspicuous, usually immersed between surface wood fibres, but sometimes ± emergent, black, *c.* 35–80 μm diam; walls dark green, K−, HNO_3+ purple-red, composed of tightly bound, pigmented hyphae, *c.* 2 μm wide. *Conidia* (*mesoconidia*) cylindrical, sometimes biguttulate, 3·9–5·5×1–1·4 μm.

Chemistry: Sections of apothecia and thallus C−; no substances detected by t.l.c.

Observations: Micarea eximia is characterized by the combination of an endoxylic thallus, small, black, ± globose or tuberculate apothecia, bright green upper hymenium, reddish or purplish brown (K+ green) hypothecium, simple or 1-septate, oblong-fusiform spores, and an absence of stalked pycnidia. It is most likely to be confused with *M. contexta* and *M. olivacea*. The former has broader, ovoid spores and a darker hypothecium; and the latter has a less brightly coloured hymenium, a darker olivaceous hypothecium, more numerous and broader paraphyses, shorter and slightly broader spores with rounded apices, and shorter mesoconidia. *M. nigella* differs from *M. eximia* in having a purplish brown upper hymenium, a darker hypothecium (hyphal walls pigmented), ellipsoid to oblong-ovoid, simple spores, and stalked pycnidia. The spores of *M. eximia* are similar to those of *M. denigrata*, but that species has an olivaceous, K+ violet pigment in its upper hymenium and pycnidial walls, and a ± hyaline hypothecium.

Habitat and distribution: M. eximia is a rare or overlooked species of conifer lignum, known only from middle Sweden and northern Finland. Associated species on the specimens examined include *Bacidia retigena, Calicium glaucellum, Cetraria pinastri, Cladonia* spp., *Lecidea pullata, Micarea misella, Parmeliopsis aleurites, P. ambigua, P. hyperopta,* and *Xylographa vitiligo*.

14. **Micarea globulosella** (Nyl.) Coppins, **comb. nov.**
(Figs 15, 43A–B; Map 24)

Lecidea globulosella Nyl., *Lich. Jap.*: 69 (1890). – *Bacidia globulosella* (Nyl.) Zahlbr., *Cat. lich. univ.* **4**: 202 (1926). Type: Japan, Yokohama, on bark, 1879, *E. Almquist* (S – lectotype!; isolectotypes: H-NYL 17412! and 17413!, S!).

Thallus effuse, of scattered or, more usually, ± contiguous areolae. Areolae convex, whitish or grey, not gelatinous when wet, 40–150 μm diam; in section without an amorphous covering layer, outer hyphae sometimes olivaceous (or brownish) and K+ violet. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia numerous, immarginate, convex and adnate to subglobose, sometimes becoming tuberculate, greyish or brownish black, sometimes pale grey or pallid (shade forms), 0·1–0·3 mm diam. *Hymenium* 35–40 μm tall, dilute olivaceous or dilute olive-brown, K+ violet. *Asci* clavate, 30–35×9–12 μm. *Spores* fusiform-acicular or ± rod-shaped, slightly curved or ± straight, 0–3(–6)-septate, 13–26×(1·5–)2–2·5(–3) μm. *Paraphyses* numerous, branched and sometimes anastomosing, *c.* 1 μm wide, sometimes widening to 1·5 μm towards their apices; apical walls hyaline. *Hypothecium* 50–70 μm tall, hyaline. *Excipulum* indistinct, evident in some sections as a narrow, reflexed, lateral border to the hymenium, hyaline or dull olivaceous (then K+ violet); hyphae radiating, branched and anastomosing, *c.* 1 μm wide.

Pycnidia frequent but inconspicuous, immersed or emergent, whitish to dark grey; walls olivaceous or dull brownish, K+ violet (especially around the ostioles), sometimes ± hyaline. Pycnidia of two types: (a) immersed within large areolae, sometimes emergent, 60–100 μm diam; *conidia* (*mesoconidia*) ± cylindrical, 3·6–5·3×1–1·4 μm; (b) similar but smaller, *c.* 30–40 μm diam; *conidia* (*microconidia*) narrowly cylindrical, 3·8–5×0·8–1 μm.

Chemistry: Thallus C+ red, K−, PD−; apothecia sections C− or C+ red (also C+ violet due to olivaceous pigment); t.l.c.: gyrophoric acid.

Observations: M. globulosella is closely related to *M. denigrata* and *M. nitschkeana* but can be distinguished by its longer, almost acicular, or rod-shaped spores. My early suspicions that *M. globulosella* could be a long-spored variant of *M. nitschkeana* were removed by the examination of microconidia, those of *M. nitschkeana* being significantly longer (mostly 5·5–7 μm). Long, curved macroconidia, as found in *M. denigrata* and *M. nitschkeana*, have not yet been found in *M. globulosella*, but they should be sought for in additional material. See under *M. synotheoides* for differences from that species and *Bacidia beckhausii.* The name *Micarea bacidiella* (a synonym of *B. beckhausii*) was mistakenly applied to *M. globulosella* by Vězda & Wirth (1976) and Poelt & Vězda (1977).

Habitat and distribution: M. globulosella is a rare but widespread species, so far known to me from Wales, Sweden, Finland, south-east France, Bavaria (Allgäu), Czechoslovakia (High Tatra), Canada (Quebec), and Japan (Honshu). It seems to prefer conifer bark, but at the Welsh locality it occurred on the top of an old gate in a wooded valley, and was accompanied by *Lecanora piniperda, Lecidea aeruginosa,* and *L. icmalea*. The specimen from Allgäuer Alpen is associated with *Graphis scripta, Menegazzia terebrata, Stenocybe major,* and *Frullania* sp. on *Abies*; that from Sweden is on *Picea* with *Cetraria pinastri* and *Ptilidium pulcherrimum*; and those from Czechoslovakia are on *Picea,* with *Cetraria chlorophylla, Hypogymnia physodes,* and *Ptilidium pulcherrimum*. At the French locality it was growing on an old basidiome of the polypore *Daedaleopsis confragosa* on *Pinus hapelensis*.

It seems to require humid conditions in old forest situations, but has a more widespread distribution than *M. synotheoides* which is strongly oceanic. *M. globulosella* may have a greater tolerance to cold winter temperatures, such as occur in the central European montane regions.

Exsiccata: Räsänen *Lichenoth. Fenn.* 426 (hb Vězda).

15. **Micarea hedlundii** Coppins, **sp. nov.**
(Figs 14C, 44A)

Thallus effusus, olivaceo-viridis, subtiliter granulosus ad 0·4 mm crassus, constatus ex goniocystis; goniocystae *c.* 20–40 μm diam, omnes cum pigmento flavo-brunneolo, K+ purpureo-violaceo et oleoso. *Algae* cellulis 4–7 μm diam. *Apothecia* vulgo pauca vel etiam nulla, immarginata, convexo-hemisphaerica mox tuberculata, pallida vel griseo-fusca demum obscure fusca, 0·15–0·5 μm diam. *Hymenium c.* 35 μm altum, ± hyalinum vel p.p. dilute olivaceo-brunneolum, K+ violaceum. *Ascosporae* ellipsoideae, ovoideae vel oblongae, simplices interdum 1- septatae, 6·5–10(–12)×2·3–4 μm. *Paraphyses* aliquantum paucae, ramosae, *c.* 0·7–1(–1·5) μm latae, apicibus vix incrassatis, incoloratis, *Hypothecium* pallidum.

Excipulum paulum evolutum. *Pycnidia* numerosa, conspicua, stipitata, 0·1–1·0 mm alta, 0·07–0·14 mm diam, cum stipibus simplicibus vel ramosis, toto griseo-brunneo vel roseo-brunneo cum tomento exili albido. *Conidia* oblongo-ellipsoidea vel oblongo-ovoidea, (4–)4·5–5·5(–6)×1·3–1·7 μm.

Typus: Norvegia, Opplandia, par. Ringebu, ad oriento-boreo-orientum ex Ringebu, ad Søråa, inter Nyhamnsbekken et Ulveslåbekken, alt. 400 m, ad truncum decorticatum, 25 viii 1979, leg. *L. Tibell* 8657 (UPS – holotypus).

Thallus epixylic or over bryophytes on lignum, effuse, dull olive-green, consisting of fine granules (goniocysts) forming a loose crust to *c.* 0·4 mm thick. Goniocysts *c.* 20–40 μm diam, the centre of each with a yellow-brown or dull orange pigment which in K appears as purple-violet oily droplets. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia few or sometimes absent, immarginate, convex and soon becoming tuberculate, pallid to grey-brown or dark brown, 0·15–0·5 mm diam. *Hymenium c.* 35 μm tall, ± hyaline with vertical streaks of straw-brown or pale olive-brown, K+ violet, C+ violet, HNO_3+ reddish; lower hymenium sometimes with dull orange, K+ purple-violet (oily droplets) pigment. *Asci* clavate, *c.* 30×12 μm. *Spores* ellipsoid, ovoid or oblong, simple, a few sometimes 1-septate, 6·5–10(–12)×2·3–4 μm. *Paraphyses* rather scanty, branched and sometimes anastomosing, 0·7–1(–1·5) μm wide, apices not swollen or pigmented. *Hypothecium c.* 70–100 μm tall, hyaline, or with dull orange, K+ purple-violet (oily droplets) pigment in upper part; hyphae interwoven, becoming vertically orientated towards the hymenium, *c.* 1–1·7 μm wide, intermixed with swollen short-celled ascogenous hyphae. *Excipulum* indistinct and soon reflexed, sometimes discernible in young apothecia as a narrow, hyaline, non-amyloid zone; hyphae radiating, branched and anastomosing, *c.* 0·8–1 μm wide.

Pycnidia numerous and conspicuous, stalked with one or to about five borne terminally on simple or branched pycnidiophores. Pycnidiophores (including pycnidia) grey-brown or pinkish brown, covered with a thin whitish tomentum, *c.* 0·1–1 mm tall and 0·07–0·14 mm diam; lower parts of pycnidophores often covered in goniocysts. Pycnidiophore and pycnidial wall tissues composed of hyaline hyphae bound by a dilute reddish brown matrix reacting K+ violet or violet-brown and HNO_3+ reddish; surface of pycnidiophores and pycnidia with protruding, slender, flexuose, hyaline tomental hyphae *c.* 0·7–1 μm wide. *Conidiogenous cells* ampulliform to ± cylindrical, 5–10×*c.* 1·5 μm, often swollen at base to 2·5 μm wide. *Conidia* (*mesoconidia*) oblong-ellipsoid or oblong-ovoid, (4–)4·5–5·5(–6)×1·3–1·7 μm.

Chemistry: Thallus C−, PD−; apothecia sections C− (but with C+ violet pigment); no substances or traces of 'prasina-unknown B' (? contaminant) detected by t.l.c.

Observations: Micarea hedlundii is readily identified by its finely granular, darkish green thallus with distinctly stalked, pinkish brown, tomentose pycnidia. Several other *Micarea* species have stalked pycnidia but in none of them are they tomentose. Another unique feature of *M. hedlundii* is the dull orange pigment, present in the goniocysts and sometimes in the lower hymenium and upper hypothecium, which appears as purple-violet oily droplets in K. Unlike the olivaceous K+ violet pigment found in this species and others (e.g. *M. denigrata, M. nitschkeana,* and *M. prasina*), it remains unchanged in C and 50% HNO_3. *M. hedlundii* is unlikely to be confused with any other *Micarea*, but is probably closely related to *M. prasina. M. anterior* has reddish brown, stalked pycnidia but they are glabrous and produce shorter conidia; in addition its apothecia and pycnidia are completely devoid of K+ violet pigments.

The chemistry of *M. hedlundii* is problematical. Of the three specimens tested by t.l.c., the type from Norway contains no detectable substances, but the two specimens from Austria (GZU) and Germany (hb Poelt) appear to contain small amounts of 'prasina-unknown B'. This substance is known elsewhere only in the type race of *M. prasina* and it is possible that its detection in the aforesaid samples is due to contamination by that species. However, the production of 'prasina-unknown B' by *M. hedlundii* is a possibility meriting further study, especially as *M. hedlundii* and *M. prasina* appear to be closely related to one another. New and carefully collected specimens of *M. hedlundii* are required to resolve this problem.

Habitat and distribution: M. hedlundii occurs on old stumps (? mainly of conifers) in woodlands. Few associated lichens are present on the specimens examined, mostly just a few scattered squamules of *Cladonia* spp. and fragments of *Lepraria* spp, although one of the Norwegian collections includes a *Chaenothecopsis*. *M. hedlundii* seems to be a very rare species, but is known from scattered localities in Norway, Sweden, Germany (Bayern), Austria (Steiermark), and possibly Switzerland.

Etymology: This new species is named in honour of Johan Teodor Hedlund (1861–1953) in recognition of his pioneering study of *Micarea* included in his doctorate thesis for the University of Uppsala (Hedlund, 1892), a work that has been a constant inspiration during my own studies.

16. **Micarea incrassata** Hedl.
(Figs 4C, 16, 41A–B; Map 3)

in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 82, 94 (1892). Type: Austria, 'supra muscos in summo jungo Kraxentrag circa Brenner, Tirol, *c.* 2800 m. alt.', *A. Minks* (S – holotype!).

Lecidea assimilata B. [var.] *infuscata* Th. Fr., *Lich. Scand.* **2**: 522 (1874). – *Lecidea assimilata* f. *infuscata* (Th. Fr.) Vainio in *Medd. Soc. Fauna Fl. fenn.* **10**: 85 (1883). Type: Norway, Sör-Tröndelag, Oppdal hd., Dovre, Kongsvoll, Högsnyta, 17 viii 1863, *Th. M. Fries* (UPS – lectotype!; UPS – isolectotype! [t.l.c.: no substances]).

Thallus growing on bryophytes, plant debris or sandy soil, composed of confluent, convex-verrucose areolae that are intermixed with cephalodia. Areolae dull grey-white, or grey-brown to dark grey, matt, 0·08–0·3 mm diam; in section, usually without a hyaline amorphous covering layer (but sometimes seen in sections of young areolae), hyphae in outer *c.* 10 μm often with light brown walls. A ± algae-free medulla often differentiated. Thallus hyphae *c.* 1·8–3 μm wide. *Phycobiont* micareoid, cells 4–7 μm diam. *Cephalodia* often present, irregularly globose and hidden amongst the areolae but sometimes visible externally as brown areolae-like structures, 0·2–0·6 mm diam; containing *Nostoc,* cells 3–5 μm diam. Less often present are irregular, rather loose clusters (? cephalodia) of *Stigonema*.

Apothecia numerous, immarginate, convex, ± adnate and often partly immersed by surrounding areolae, black, matt, 0·3–0·8(–1) mm diam, sometimes forming irregular tuberculate clusters up to 1·2 mm diam. *Hymenium* 45–50 μm tall; upper *c.* 10 μm (epithecium) dark aeruginose or olivaceous, K–, HNO_3+ red; remaining (lower) part dilute greenish or hyaline. *Asci* clavate, 45–48×11–14 μm. *Spores* ellipsoid, oblong-ellipsoid, oblong-ovoid or oblong-fusiform, 0–1(–2)-septate, (10–)12–17×4–4·8 μm. *Paraphyses* numerous, simple below, sometimes forked above, sometimes anastomosing, (1–)1·5–2 μm wide, sometimes widening above to 3 μm; apical walls hyaline although surrounded by dense pigment in the surrounding gel matrix. *Hypothecium c.* 150–400 μm tall, sometimes 'rooting' to the base of the adjoining areolae, dark red-brown, without a purple tinge, K–, HNO_3+ bright orange-brown; hyphae interwoven, or ± vertically arranged in upper part, *c.* 1·7–2·5(–3) μm wide, surrounded by densely pigmented matrix; ascogenous hyphae *c.* 2·5–5 μm wide. *Excipulum* indistinct, sometimes evident as a reflexed, dull olivaceous or reddish brown zone; hyphae radiating, branched and anastomosing, *c.* 1–2 μm wide.

Pycnidia rare, immersed to sessile, black, 30–60 μm diam; walls dark green above, changing to reddish brown at base; *conidia* (? *microconidia*) cylindrical or cylindrical-fusiform, 6–9×1–1·3 μm.

Chemistry: Thallus K–, C–, PD–; t.l.c.: no substances.

Observations: See *M. assimilata*.

Habitat and distribution: M. incrassata occurs in much the same habitats as *M. assimilata* but appears to be more widely distributed. In Europe it has an arctic-alpine distribution ranging from Spitzbergen (*c.* 79°N) in the high arctic, southwards to the Kola peninsula, central Norway (Opland), and central Sweden (Härjedalen). Further south it occurs in the Scottish highlands (Clova in Angus, and near Loch Merkland in East Sutherland), Denmark, and the Alps (Upper Bavaria, Austrian Tirol, and Switzerland). I have not seen it from Alaska or Canada although it probably occurs in those regions. From further south in North America it has been collected at altitudes of *c.* 3400–3900 m in the Rocky Mountain National Park in Colorado by Anderson (1964). *M. incrassata* has been collected on Kerguelen Island in the southern Indian Ocean (48°30′S) and is so far the only arctic or arctic-alpine *Micarea* known to have a bipolar distribution.

Exsiccata: Fellman *Lich. Arct.* 164 (BM ex K, H, H-NYL 16567), 166 (BM ex K, H).

17. **Micarea intrusa** (Th. Fr.) Coppins & Killias, **comb. nov.**
(Figs 17, 55; Map 22)

Lecidea intrusa Th. Fr. in *Bot. Notiser* **1867**: 152 (1867). – *Catillaria intrusa* (Th. Fr.) Th. Fr., *Lich. Scand.* **2**: 579 (1874). – *Lecidiopsis intrusa* (Th. Fr.) Zopf in *Hedwigia* **35**: 338 (1896). – *Conida intrusa* (Th. Fr.) Sacc., *Syll. Fung.* **18**: 187 (1906). Type: Finland, Tavastia australis, Mustiala, 1867, *A. Kullhem* (UPS – holotype!).

Lecidea aphanoides Nyl. in *Flora, Jena* **51**: 476 (1868). Type: Scotland, South Aberdeenshire, Braemar, 'Craig Guie', viii 1868, *J. M. Crombie* (H-NYL 20237 – holotype!); supposed isotype material in BM appears to be all *Scoliciosporum umbrinum* (Ach.) Arnold.

Lecidea melaphana Nyl. in *Flora, Jena* **52**: 83 (1869). Type: Scotland, South Aberdeenshire, Braemar, 'Craig Guie', viii 1868, *J. M. Crombie* (BM – isotype!).

Lecidea contrusa Vainio in *Medd. Soc. Fauna Fl. fenn.* **10**: 29 (1883); *nom. illeg.* (Art. 63).

Thallus occasionally effuse but more often forming small patches (to *c.* 1 cm diam) amongst other lichens, irregularly granular-verrucose and often rimose, sometimes forming discrete areolae (*c.* 0·1–0·3 mm diam) which may coalesce to form 'composite areolae' up to *c.* 1 mm diam and 0·5 mm tall. Thallus dark olive-grey or brownish grey; surface matt, and usually scurfy due to invasion of free-living algae. In section, sometimes with a hyaline amorphous covering layer up to 12 μm thick but this is usually disrupted by invading algae; walls of uppermost hyphae sometimes thickened with olive-green pigment, K−, HNO_3+ red; phycobiont layer *c.* 70–100 mm thick, above a ± distinct hyaline medulla. *Phycobiont* not micareoid; cells globose, large, 7–21 μm diam, with thick hyaline walls 1–2 μm thick, each cell deeply penetrated by a haustorium of the mycobiont (Fig. 55).

Apothecia numerous, immarginate, convex, adnate, black, or slightly glossy when young, 0·14–0·4 mm diam. *Hymenium* 40–50 μm tall; upper (*c.* 20 μm) part aeruginose-green, K−, HNO_3+ red; remaining (lower) part ± hyaline. *Asci* clavate, 35–45×14–15 μm; cytoplasm of asci and spores sometimes with an orange, K+ purple-red pigment. *Spores* ellipsoid or ovoid-ellipsoid, occasionally oblong-ellipsoid or oblong fusiform and then sometimes slightly curved, simple or 1-septate and septum often eccentric, rarely 3-septate (7–)9–14(–17)× (4–)4·5–5·5(–6) μm. *Paraphyses* numerous, branched and anastomosing, *c.* 1–1·5(–1·7) μm wide; apices not swollen or pigmented (green pigment confined to the surrounding gel-matrix). *Hypothecium c.* 110–200 μm tall, hyaline or with very faint olivaceous brown tinge in places,

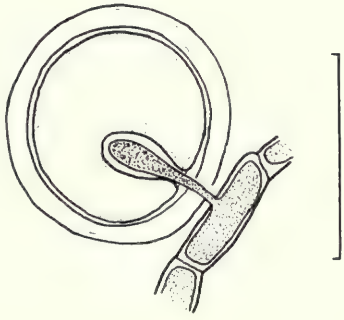


Fig. 55 *Micarea intrusa*: a phycobiont cell penetrated by a haustorium of an associated mycobiont hypha. Scale = 10 μm.

upper part sometimes pale orange, K+ purple-red (see below); hyphae interwoven, but becoming vertically orientated towards the hymenium, hyaline, *c.* 1·7–2 μm wide; ascogenous hyphae short-celled, to 5 μm wide, contents sometimes with dilute orange, K+ purple-red pigment. *Excipulum* reflexed to below the surface of surrounding thallus, thin, dilute brownish or ± hyaline in places, sometimes darkish brown at outer edge; hyphae radiating, branched and anastomosing, *c.* 1·5–2 μm wide.

Pycnidia not seen.

Chemistry: Thallus surface and sections K−, C−, KC−, PD−, I−; apothecia sections C−; not analysed by t.l.c.

Observations: This species is placed in *Micarea* with some hesitation, owing to its unusual habitat (for a *Micarea*) and large-celled, thick-walled, non-micareoid phycobiont. However, much the same habitat is shared by *M. subnigrata* (a species with a typical micareoid phycobiont) and no other fungal characters appear to merit its exclusion. It is similar in appearance to *M. subnigrata* which can be distinguished by its brown epithecium and usual presence of pycnidia containing helicoid macroconidia. Superficially, *M. intrusa* is virtually indistinguishable from

Table 5 Species associated with *Micarea intrusa* in Norway (see text).

	± vertical rocks	± horizontal rocks
Aspicilia morioides		+
Caloplaca cf. *lamprocheila*	+	
Candelariella vitellina	+	
Cornicularia normoerica		+
Fuscidea cyathoides	+	
F. intercincta	+	
F. tenebrica	+	
Haematomma ochroleucum	+	
Lecanora badia	+	+
L. gangaleoides	+	
L. intricata		+
L. polytropa	+	
L. cf. *salina*	+	
Lecidea fuliginosa	+	+
L. fuscoatra		+
L. lactea	+	+
L. lapicida	+	
L. leucophaea		+
L. vorticosa		+
Micarea subnigrata	+	
Opegrapha gyrocarpa	+	
Pertusaria dealbescens		+
P. lactea		+
Placopsis gelida	+	
Porina chlorotica	+	
P. guentheri	+	
Ramalina subfarinacea	+	
Rhizocarpon geographicum	+	+
R. lecanorinum		+
R. riparium subsp. *lindsayanum*		+
Rinodina gennarii	+	
Schaereria tenebrosa		+
Stereocaulon vesuvianum		+
Trapelia involuta	+	
Umbilicaria spodochroa		+

forms of *Scoliciosporum umbrinum* with a well developed thallus, but that species has vermiform or sigmoid-curved spores. The phycobiont in *M. intrusa* and *S. umbrinum* appears to be the same; any future critical appraisal of the delimitation of *Scoliciosporum* should seriously consider the generic disposition of *M. intrusa*.

The pale orange, K+ purple-red pigment commonly found in the ascogenous hyphae, asci and spores has not been seen by me in any other *Micarea*, although it is conceivable that it is the same, or similar, to the pigment found in the goniocysts of *M. hedlundii* (*q.v.*).

Habitat and distribution: M. intrusa occurs on hard siliceous (igneous) rocks in communities referable to the *Umbilicarietum cylindricae* in its broad sense (James *et al.*, 1977). In Nylander's protologue of *Lecidea aphanoides* it is said to occur on calcareous rock, but this is erroneous; application of 50% HNO_3 to fragments of substratum from the holotype produced no effervescence. The formation of small patches amongst other crustose lichens indicates that *M. intrusa* may be, at least facultatively, parasitic. Such suggestions have been previously propounded by Magnusson (1942), Poelt (1958), and Wirth (1973), all of whom related its behaviour to that of *Lecanora intrudens* and *Lecidea furvella*. In several collections, including the type of *Lecidea intrusa*, it occurs amongst the areolae of *Huilia panaeola*, but it is by no means confined to that 'host'.

From her studies on the island of Sotra in Hordaland, Norway, Miss L. Skjolddal informs me that *M. intrusa* occurs on sheltered, sunny, west or south-west facing exposures of gneiss and amphibolite, on steep surfaces or, in one case, on a ± horizontal surface. Miss Skjolddal kindly provided me with a list of associated species (Table 5).

M. intrusa is probably widespread in areas of western Europe with exposed, hard, igneous rocks; however, it is a very inconspicuous species and records are wanting from many potential localities. I have seen material from southern Scandinavia (several localities), North Norway (Finnmark), and the Grampian Mountains of Scotland. In addition, Wirth (1973) cites collections from France (Vosges) and West Germany (Schwarzwald).

Exsiccata: Norrlin & Nyl. *Herb. Lich. Fenn.* 182 (BM).

18. **Micarea leprosula** (Th. Fr.) Coppins & A. Fletcher
(Figs 18, 53–54; Map 8)

in Fletcher in *Lichenologist* **7**: 111 (1975). – *Bilimbia milliaria* γ *leprosula* Th. Fr., *Lich. Scand.* **2**: 382 (1874). – *Micarea violacea* var. *leprosula* (Th. Fr.) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 81, 92 (1892). – *Bilimbia leprosula* (Th. Fr.) H. Olivier in *Bull. Géogr. bot.* **21**: 179 (1911). – *Bacidia leprosula* (Th. Fr.) Lettau in *Hedwigia* **52**: 133 (1912). Type: Sweden, Uppsala, Witulfsberg [Wittulsberg], 26 vi 1852, *Th. M. Fries* (UPS – lectotype! [t.l.c.: argopsin and gyrophoric acid]).

Thallus effuse, superficial, of convex to subglobose areolae *c.* 100–350(–400) μm diam; these usually coalesce toward the centre of the thallus, whence they may proliferate, producing secondary granular-areolae, such that the thallus becomes thicker (to *c.* 700 μm thick). Areolae blue-grey or, more rarely, grey-brown, matt with a minutely roughened surface with white flecks (×50 lens); lower sides of ± globose areolae, and areolae in shaded situations, often unpigmented and greenish white. Areolae fragile and often breaking down or eroding to form sorediate patches with irregularly shaped soredial granules *c.* 20–50 μm diam. Sections of intact areolae ecorticate and without an amorphous hyaline covering layer; outermost hyphae often coloured with greenish or brownish pigment, K−, HNO_3+ reddish. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia often absent, at first adnate but often becoming constricted below, convex to subglobose, commonly tuberculate, immarginate or rarely very faintly marginate when young, matt or slightly glossy, dark blue-grey or black, 0·15–0·4 mm diam, or to 0·7 mm diam when tuberculate. *Hymenium* 45–60 μm tall, hyaline or dilute green, but dark green (K−, HNO_3+ red) in upper part (epithecium). *Asci* clavate, 40–55×14–16 μm. *Spores* oblong-ellipsoid, oblong-fusiform or clavate-fusiform, often curved, (1–)3-septate, 14–26(–29)×4–5(–5·5) μm. *Paraphyses* numerous, branched and anastomosing, (0·7–)1–1·5 μm wide; apices often more richly branched, not or only slightly incrassate (to 1·8 μm wide) and without closely adhering pigment (epithecial pigment confined to surrounding gel-matrix). *Hypothecium c.* 35–45 μm tall, but becoming much taller in markedly convex or tuberculate apothecia, dilute straw- or fuscous-brown, pigment confined to gel matrix; hyphae interwoven, but becoming outwardly orientated towards the hymenium and excipulum, *c.* 0·8–1·5 μm wide; ascogenous hyphae with swollen cells, *c.* 2–6 μm wide. *Excipulum* distinct in young, moderately convex apothecia, but reflexed and obscured in subglobose or tuberculate apothecia, dilute fuscous brown (K−); hyphae radiating, branched and anastomosing, *c.* 0·5–1·5 μm wide.

Pycnidia not found.

Chemistry: Thallus K−, C+ red, PD+ red; apothecia in section C+ red; t.l.c.: argopsin and gyrophoric acid.

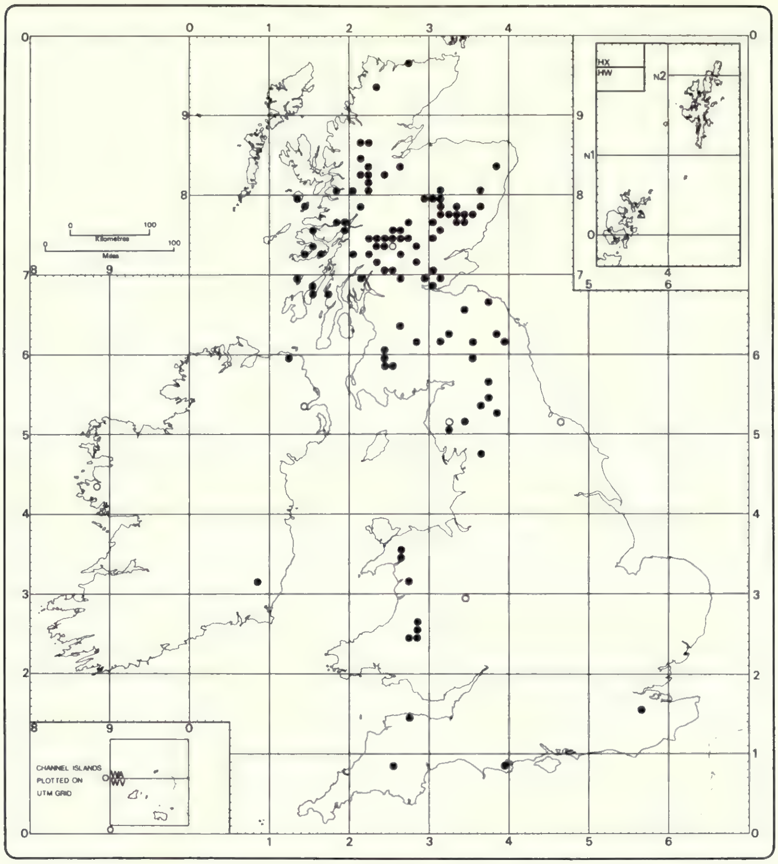
Observations: M. leprosula is characterized by its sterile or sparingly fertile, granular thallus composed of blue-grey (or brown-grey), fragile areolae which often dissolve (or become abraded) to form contrasting, yellowish green, sorediose patches. These characters are shared by the much rarer *M. subleprosula*, and the thalli of both react C+ red. However, *M. subleprosula* can be separated by the PD+ yellow reaction of its thallus due to the presence of alectorialic acid. When fertile *M. subleprosula* is found to have much larger, mostly 7-septate spores. *M. leprosula* is usually distinctive in the field (although material should always be checked with *M. subleprosula* in mind) but can easily be overlooked when it occurs on bryophytes on shaded rocks or trees, whence the thallus often lacks its characteristic bluish tinge and the areolae are thinly scattered. The species is usually sterile but fertile specimens are occasionally encountered, especially in sheltered (but not deeply shaded) situations, such as on boulders and old walls in woodland.

Hedlund (1892) regarded *M. leprosula* as a variety of *M. peliocarpa* (*q.v.*) and the apothecia of the two species are somewhat similar. However, those of *M. leprosula* exhibit several minor, yet significant, differences; spores tend to be slightly longer; apothecia tend to be more markedly convex and more frequently tuberculate; hypothecium and excipulum are dilutely pigmented with a dull brown pigment; and paraphyses never become thickened and pigmented at their apices. The two species also differ in several fundamental aspects of thallus morphology and chemistry. With regard to the production of argopsin and to the presence of a dull brown pigment in the excipulum and hypothecium *M. leprosula* shows some affinity to *M. lignaria* var. *lignaria*, with which it often occurs. However, *M. lignaria* lacks gyrophoric acid, has usually longer and more septate spores, and somewhat stouter and only sparingly branched paraphyses. The areolae of *M. leprosula* and *M. subleprosula* differ from those of such species as *M. lignaria, M. peliocarpa,* and *M. cinerea,* in lacking an amorphous hyaline covering layer (see 'morphology').

Habitat and distribution: M. leprosula is widely distributed in upland areas in the north and west of Britain, occurring at altitudes from about sea-level to at least 1100 m. It is found, usually on moribund bryophytes (e.g. *Andraea* spp. and *Rhacomitrium* spp.) on rocky ledges, boulders, and old walls, in exposed hilly areas, mountain sides or woodlands. Associated lichens noted amongst British collections include *Arthrorhaphis citrinella, Baeomyces rufus, Belonia incarnata, Cladonia cervicornis, C. coccifera, C. crispata, C. portentosa, C. squamosa, C. subcervicornis, Coelocaulon aculeatum, Lecidea granulosa, L. icmalea, Lepraria neglecta, Micarea lignaria, M. peliocarpa,* and *Vorarlbergia renitens.* From Scotland I have seen two corticolous specimens, on trunks of *Alnus* and *Betula*; associated species present included *Cladonia coniocraea, C. squamosa, Lecidea icmalea, Micarea melaena,* and *Platismatia glauca*.

There are two outlying localities in the lowlands of southern England. In Dorset it occurs on waste heaps of slag clay with *M. lignaria* (*q.v.*); and in Kent it was found with *M. peliocarpa* on wood chips lying at the side of a woodland track in a chestnut (*Castanea*) coppice.

M. leprosula is poorly recorded outside Britain, probably because it is so often sterile. To date, I have seen one specimen from Norway (Hordaland) and several collections from mid- and southern Sweden. Further south it seems to be well represented in the Alps, and I have seen one



Map 8 *Micarea leprosula* ● 1950 onwards ○ Before 1950

collection from Bohemia (Czechoslovakia). This Bohemian record, and another from the Black Forest (Schwarzwald) were made from exsiccate specimens (*Kuták* 417 and *Migula* 1) of *M. lignaria* growing on wooden roof shingles.

Exsiccata: Kuták *Lich. Bohem.* 417 *p. min. p.* (0). Magnusson *Lich. Sel. Scand.* 208 (BM, C, GZU). Migula *Crypt. Germ.* 1 *p. min. p.* (C, E, M).

19a. **Micarea lignaria** (Ach.) Hedl. var. **lignaria**
(Figs 1A, 3D–E, 19, 45, 53–54; Map 9)

in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 82, 93 (1892). – *Lecidea lignaria* Ach. in *K. svenska VetenskAkad. Handl.* **1808**: 236 (1808). – *Bilimbia lignaria* (Ach.) Massal., *Ric. Lich. Crost.*: 121 (1852). – *Bacidia lignaria* (Ach.) Lettau in *Hedwigia* **52**: 132 (1912). Type: Sweden: 'Svecia', on lignum, (H-ACH 265 – lectotype; BM – ? isotype!).

Lecidea milliaria Fr. in *K. svenska VetenskAkad. Handl.* **1822**: 255 (1822). Type: Sweden, Småland, Femsjö, on lignum, *E. M. Fries* (UPS – lectotype! [t.l.c.: argopsin]).

Lecidea geomaea Taylor *in* Mackay, *Fl. Hib.* **2**: 124 (1836). Type: Ireland, South Kerry, Dunkerron, *T. Taylor* (BM – lectotype!; BM ex K – isolectotype!).

Bilimbia milliaria α. [var.] *lignaria*** [f.] *calamophila* Körber, *Parerga lich.*: 171 (1860). Type: Germany: 'an Schilfrohrdächern um Münster', *J. G. F. X. Lahm* (L 910, 144–1685 – lectotype!; L 910, 144–1689 – isolectotype! [t.l.c.: argopsin].

Bilimbia milliaria β. [var.] *saxicola* Körber, *Parerga lich.*: 171 (1860). Type: Germany: 'Bilimbia trochiscus Körb. prim, B. millaria β. saxicola Kb.! Extersteine', on sandstone, ? *Beckhaus* (WRSL – lectotype!).

Paratype: Germany: 'Ibbenbüren in Westfalen, Lahm, Hb. Hepp.', on sandstone (BM!).

Stereocauliscum gomphillaceum Nyl. in *Flora, Jena,* **48**: 211 (1865). – *Micarea gomphillacea* (Nyl.) Vězda in *Folia geobot. phytotax., Praha* **5**: 321 (1970). – *Bilimbia milliaria* f. [as 'f?'] *gomphillacea* (Nyl.) Blomb. & Forss., *Enum. Pl. Scand.*: 82 (1880). – *Micarea lignaria* [as *'ligniaria'*] f. *gomphillacea* (Nyl.) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 94 (1892). Type: Finland, Tavastia australis, Hollola, Tiirismaa, Pirunpesä, [on granite rock], 1863, *J. P. Norrlin* (H-NYL 40217 – lectotype! [t.l.c.: argopsin]; isolectotypes: H-NYL 40214!, 40215!, 40216!, 40218! and p.m. 631!).

Lecidea sabuletorum var. *milliaria* f. *nigrata* Nyl. in *Not. Sällsk. Fauna Fl. fenn. Förh.* **8**: 151 (1866). Type: USSR, Kola Peninsular, Lapponia ponojensis, Ponoi, 1863, *N. I. Fellman* (H – holotype!; H – isotype!). See note (i) below.

Lecidea milliaria var. *triseptata* Nyl. *in* Lamy in *Bull. Soc. bot. Fr.* **25**: 441 (1878). – *Bilimbia triseptata* (Nyl.) Arnold in *Flora, Jena* **67**: 572 (1884), non *Bacidia triseptata* (Hepp in Zoll.) Zahlbr. Type: France: Haute Vienne, 'Sur des roches entre Chalard et St Junien, *Lamy* (H-NYL 18367! – lectotype, as 'L. milliaria var. 3-septata Nyl.'). See note (ii) below.

Lecidea meizospora Harm. in *Bull. Séanc. Soc. Sci. Nancy* II, **33** (1898): 63 (1899). – *Bacidia meizospora* (Harm.) Zahlbr., *Cat. lich. univ.* **4**: 122 (1926). Type: France, Vosges, Docelles, on *Calluna* roots, *V. and H. Claudel & F. J. Harmand* (ANGUC – lectotype!).

Lecidea trisepta var. *polytropoides* Vainio in *Ark. Bot.* **8** (4): 106 (1909). Type: USSR, Magadanskya Oblast (N.E. Siberia), 'Pitlekai, peninsula Jinretlen' [*c.* 67°7'N 173°24'W], on plant debris, 1878–9, *E. Almquist* (TUR-VAINIO 21274, fertile part – lectotype!). See note (iii) below.

Patellaria milliaria var. *xylophila* Wallr., *Fl. crypt. Germ.* **1**: 349 (1831); *nom. inval.* (Art. 26).

Lecidea milliaria var. *saxigena* Leighton, *Lich. Brit. Exs.* 210 (1856); *nom. nudum* (Art. 32); see note under *M. peliocarpa*. Type: England, Shropshire, Neescliff [Nesscliff] Hill, *Leighton, Lich. Brit. Exs.* 210 (E – lectotype!; isolectotypes: BM! DBN! MANCH! NMW!).

Notes: (i) The type material mainly consists of the black stroma of *Bryomyces gymnomitrii* Döbb. on *Gymnomitrium* sp., with only a few apothecia of *M. lignaria* present.

(ii) Lamy (*loc. cit.*) gives the locality as 'entre le Chalard et Saint-Yrieix'. The label on the lectotype specimen is entirely in Nylander's handwriting and there may have been an error in transcription.

(iii) Vainio's diagnosis included the description of soralia. A small portion of the type specimen is a sterile sorediate thallus (C–, PD–; phycobiont cells 7–14 μm diam) but it is not a *Micarea* and is not part of the larger, fertile portion. The latter belongs to *Micarea lignaria* and is chosen as lectotype.

Thallus effuse, partially endoxylic or endocuticular, but more usually developed superficially as convex to ± globose areolae. Areolae *c.* 80–250(–300) μm diam, discrete, scattered to contiguous, sometimes coalescing to form an uneven crust, grey-white and ± glossy to grey-green or bluish grey and matt, sometimes brown-grey due to the ramification through their surface of brown, toruloid hyphae (cells *c.* 5–7×4·5–7 μm) belonging to an unknown fungus. Areolae in section, with a hyaline amorphous covering layer (*c.* 4–12 μm tall); walls of hyphae in outermost (exposed) parts often blue-green (K–, HNO_3+ red); algal layer usually in direct contact with substratum, but in larger areolae the algal layer may be *c.* 90–135 μm tall lying above a medulla. Medulla, when present, up to *c.* 100 μm tall, consisting of loosely interwoven hyphae *c.* 1–1·5 μm wide, intermixed with dead algal cells and debris derived from the substratum. *Phycobiont* micareoid, cells *c.* 4–7 μm diam.

Apothecia scattered, more usually numerous and crowded, often confluent, immarginate, convex-hemispherical, soon becoming constricted at the base and hence ± globose, occasionally becoming stipitate with a grey-black 'stipe' up to 1 mm tall ('f. *gomphillacea*'), black, matt or slightly glossy, rarely blue-grey (shade forms), 0·15–0·6(–0·9) mm diam. *Hymenium* 50–75 μm, often not sharply delimited from the hypothecium, dilute olivaceous or aeruginose-green (K–, HNO_3+ red) in upper, and sometimes lower, part(s) (the middle part often being ± hyaline); in the uppermost part (epithecium) the pigment is more dense and is present not only in the gel matrix but also in the walls of the paraphyses; in reflexed parts of the hymenium towards the base of the apothecium the green pigment is often replaced by a dilute brown pigment; minute (less than 2×1 μm) granules of violet (K+ intense aeruginose) pigment are sometimes present and lightly scattered through the hymenium. *Asci* clavate, 45–50×11–19 μm. *Spores* fusiform, straight or slightly curved, (0–)3–7 septate, 16–36(–38)×4–6(–7) μm. *Paraphyses* numerous, simple or slightly branched above, but more richly branched in the transition zone between the hymenium and excipulum, sometimes anastomosing, 1·3–1·8 μm wide; apices often slightly incrassate and coloured with green or greenish brown pigment and then up to 3 μm wide, usually coherent (even in K) and, together with the surrounding pigmented matrix, form an epithecium. *Hypothecium* c. 100–230(–350) μm tall, dilutely pigmented with pigment confined to gel matrix; upper part dull aeruginose or olive-brownish K− or + dulling, HNO_3+ reddish); lower part often without greenish tinge, and then being dilute brownish or ± hyaline; hyphae interwoven or some ± vertically orientated near the hymenium, *c.* 1–1·7 μm wide; ascogenous hyphae with short, swollen cells *c.* 2·5–4 μm wide. *Excipulum* ± distinct in sections of young, hemispherical apothecia, but soon becoming strongly reflexed and not sharply delimited from the hymenium, dilute brown or sometimes darkish brown along the outer edge. Hypothecial and excipular tissues sometimes elongated vertically to form a stipe ('f. *gomphillacea*').

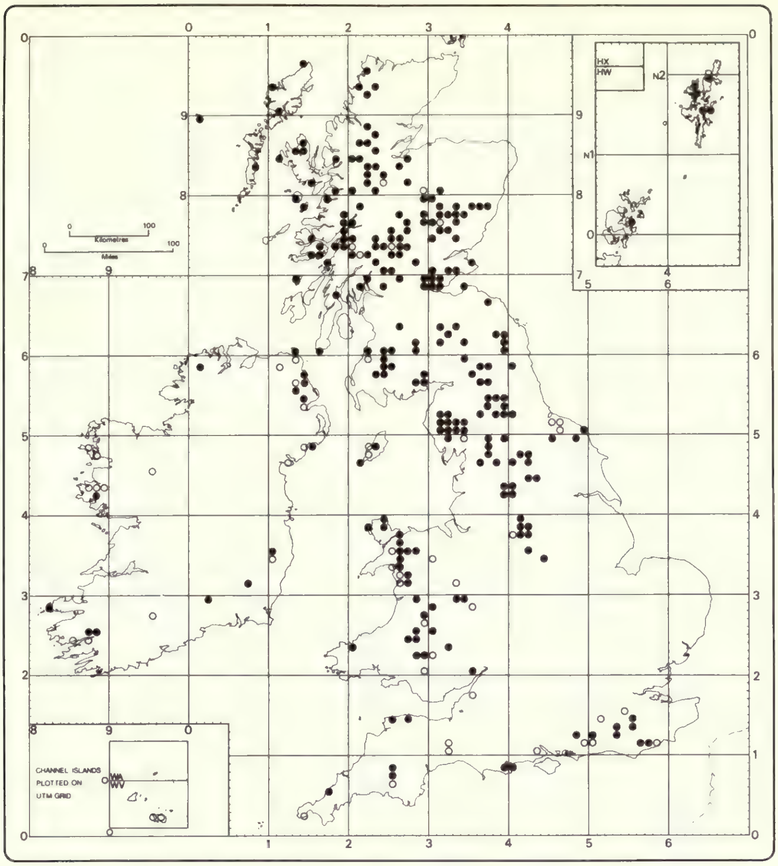
Pycnidia inconspicuous, ± immersed, with walls green (K−, HNO_3+ red) in exposed upper parts and ± hyaline in immersed lower parts; of three types [only type (c) is common]: (a) *c.* 100 μm diam; *conidia* (*macroconidia*) curved or hamate, 0–3-septate, 16–22×*c.* 1 μm; (b) *c.* 100–140 μm diam; *conidia* (*mesoconidia*) ± cylindrical, oblong-ellipsoid, obovoid or oblong-obovoid, usually distinctly truncate at proximal end, often 2–3-guttulate, 4–7(–7·6)×1·2–1·8 μm; (c) *c.* 40–50 μm diam; *conidia* (*microconidia*) narrowly cylindrical, only faintly truncated at proximal end, eguttulate, (4·5–)5–7(–8)×0·8–1 μm.

Chemistry: Thallus K−, C−, KC−, PD+ red; sections of apothecia C−, PD−; t.l.c.: argopsin.

Observations: Micarea lignaria is characterized by its whitish to grey, convex to ± globose areolae which are PD+ red (argopsin; but see var. *endoleuca*), black, markedly convex to ± globose apothecia, green upper hymenium, dilute greenish or dilute olive-brownish hypothecium, and 3–7-septate, fusiform spores. When on lignum the thallus is often reduced to small scattered areolae and sometimes it is ± entirely endoxylic. The apothecia are less variable in appearance, and pale (shade) forms are very rare. However, the apothecia are occasionally found (especially on rock in dry underhangs) to be stipitate with a 'stipe' (composed of vertically extended hypothecial and excipular tissues) up to 0·4 mm, or even 1 mm, tall (Fig. 3E). These forms have been ascribed the status of form, variety, species and even genus, viz.: Nylander's new species and genus *Stereocauliscum gomphillaceum.* In the type material of this, some 'stipes' are extremely tall (up to 1 mm) and composed of vertically proliferating apothecia, with the apical apothecia being the youngest; the apothecia are immature (or arrested in their development) with few asci and spores. In my opinion these stalked forms of *M. lignaria* result from abnormal development in response to adverse environmental conditions and are, therefore, not worthy of taxonomic recognition at any rank.

M. lignaria is often confused with *M. cinerea* and *M. peliocarpa*, but these two species have usually more flattened and often paler apothecia, more richly branched paraphyses, and a hyaline hypothecium. In addition, they contain gyrophoric acid, resulting in the C+ orange-red (quickly fading), PD− reactions of their thalli and apothecia. *M. ternaria* (*q.v.*) is very similar to *M. lignaria*, but has more flattened apothecia with a more discernible excipulum and spores which are never more than 3-septate; furthermore, it lacks any lichen substances.

Habitat and distribution: M. lignaria occurs on a wide range of substrata, but is most common in upland districts, growing over bryophytes or plant debris on siliceous rocks and walls, or on exposed peaty ground. Associated lichens found in such habitats in Britain include *Arthrorhaphis citrinella, Baeomyces rufus, Cladonia coccifera, C. floerkeana, C. squamosa, C. subcervicornis, Coelocaulon aculeatum s. lat., Lecidea granulosa, L. icmalea, Lecidoma demissum, Lepraria neglecta, Micarea leprosula, M. peliocarpa, Ochrolechia frigida, Parmelia saxatilis,* and *Pseudephebe pubescens.* It often grows over bryophyte mats that are heavily invaded by gelatinous algae, and in such situations in Scotland it has been found with the rare, or overlooked, *Arctomia delicatula* and *Belonia incarnata.* When growing directly on rock *M. lignaria* is mostly confined to sheltered, shaded situations and is sometimes present in the *Micareetum sylvicolae* in rock underhangs. It is usually present in abundance in the old lead and zinc mine workings of the Pennines and Scotland, where it grows over decaying bryophytes and



Map 9 *Micarea lignaria* var. *lignaria* ● 1950 onwards ○ Before 1950

plant debris, loose stones, pieces of timber and sack-cloth. Mr V. Giavarini has recently found it in Dorset, growing on waste heaps of slag clay, in the company of *M. leprosula, Baeomyces roseus, Cladonia arbuscula, C. ciliata, C. furcata, C. portentosa,* and *Coelocaulon aculeatum s. lat. M. lignaria* is very rare in the lowlands of south-east England, but has been found there growing directly on the rock of east or north facing sandstone walls and churchyard memorials, and also on natural sandstone outcrops of the Sussex Weald.

In upland areas *M. lignaria* is frequently found on the exposed lignum of fallen trunks (especially of conifers) and old timberwork, with, for example, *Cladonia* spp., *Hypogymnia physodes, Micarea peliocarpa, Mycoblastus sterilis, Ochrolechia turneri, Parmelia saxatilis,* and *Lecanora polytropa* (worked timber). Occurrences of *M. lignaria* on the bark of healthy trees are rather rare, and in Britain are confined to the high rainfall areas of the north and west, where it has been collected on *Alnus, Betula, Fraxinus, Ilex, Quercus,* and old *Sambucus*.

Reports of *M. lignaria* on mosses on limestone rocks usually result from the misidentification of *Bacidia sabuletorum* or *Toninia lobulata*. However, on a few occasions I have seen *M. lignaria* growing on thick bryophyte cushions or mats at high altitudes over limestone in the north Pennines, and over calcareous mica-schist in the Breadalbane Mountains; in such situations the pH and calcium content of the substratum is presumably kept low by the leaching effect of the high rainfall in those areas.

The altitude range of *M. lignaria* in Britain is from sea-level to about 1200 m (Ben Lawers), although it may well occur at higher altitudes in the Ben Nevis group and the Cairngorm Mountains. Higher altitudes are attained in the mountains of central Europe, from where it has been collected at 2800 m in the Austrian Tirol, *c.* 2000 m in the Tatry mountains of Poland and Czechoslovakia, and at nearly 2500 m in the Transylvanian Alps of Romania.

M. lignaria is common in northern and western Britain, but is very rare, with only a few scattered records, in lowland, southern England east of Devon. It is widely distributed throughout most of Europe, although in southern Europe it appears to be confined to the mountains: like most species of *Micarea* it seems to avoid the lowland Mediterranean regions. Records suggest that it is rare in arctic Fennoscandia, although I have seen material from north Finland and the Kola Peninsula. It has been found in the Azores at altitudes of about 900 m but I do not know of it from elsewhere in Macaronesia. From outside Europe I have seen material from the north coast of western Siberia, the Franconia Mountains (at *c.* 1450 m) of New Hampshire in the USA, and from Brazil (Serra Montiqueira, at *c.* 1900 m).

Exsiccata: Anzi *Lich. Lang.* 148 (BM). Arnold *Lich. Exs.* 348A, B (BM ex K, L, M). Bohler *Lich. Brit.* 85 (E). Claudel & Harm. *Lich. Gall.* 43 (BM). Cumm. Dec. *N. Am. Lich.* ed. I: 302 (BM, C), ed. 2: 232 (M). Flotow *Lich. Exs.* 129A, E and 131 (UPS). Fries *Lich. Suec.* 29 (E, M, UPS); 98 (E). Harm. *Guide* 91 (UPS). Harm. *Lich. Loth.* 852 (M). Hav. *Lich. Norv.* 555 (C). Hertel *Lecid.* 34 (E, GZU). Johnson *Lich. Herb.* 453 (E). Kalb *Lich. neotropici* 22, 186 (hb Kalb). *Krypt. Exs. Vindob.* 658 (BM, BM ex K, C, M). Kuták *Lich. Bohem.* 417 (O). Larb. *Lich. Caes. Sarg.* 83 (BM). Larb. *Lich. Herb.* 272 (BM). Leighton *Lich. Brit.* 210 (BM, DBN, E, MANCH, NMW), 238 *p.p.* (BON, DBN, E, M, MANCH), 386 (BM, BON, DBN, E, FRS, M). Lojka *Lich. Hung.* 61 (BM, BM ex K, M). Malme *Lich. Suec.* 288 (C, M, S). Migula *Crypt. Germ.* 1 *p.p.* (BM, C, M, MANCH); 226 (BM, C, MANCH). Moug. & Nestl. *Stirp. Crypt.* 1430 (E). Mudd *Lich. Brit.* 156 (BM, E, M, MANCH), 157 (E, MANCH), 158 (BM, E, M, MANCH). Norrlin & Nyl. *Herb. Lich. Fenn.* 319A, B (BM, C, H). Oliv. *Lich. Orne* 344 (M, S). Pišút *Lich. Slov.* 156 (BM, M). Rabenh. *Lich. Eur.* 322, 603 (BM, M). Roum. *Lich. Gall.* 193 (BM), 232 (BM, M). Samp. *Lich. Port.* 147 (LD). Schaerer *Lich. Helv.* 196 *p.p.* (BM, BM ex K, E). Vězda *Lich. Bohem.* 133, 258 (LD, M). Vězda *Lich. Sel.* 516, 858, 1036, 1088 (BM). Zwackh. *Lich. Exs.* 121 (BM).

19b. **Micarea lignaria** var. **endoleuca** (Leighton) Coppins, **comb. nov.** (Figs 53–54; Map 10)

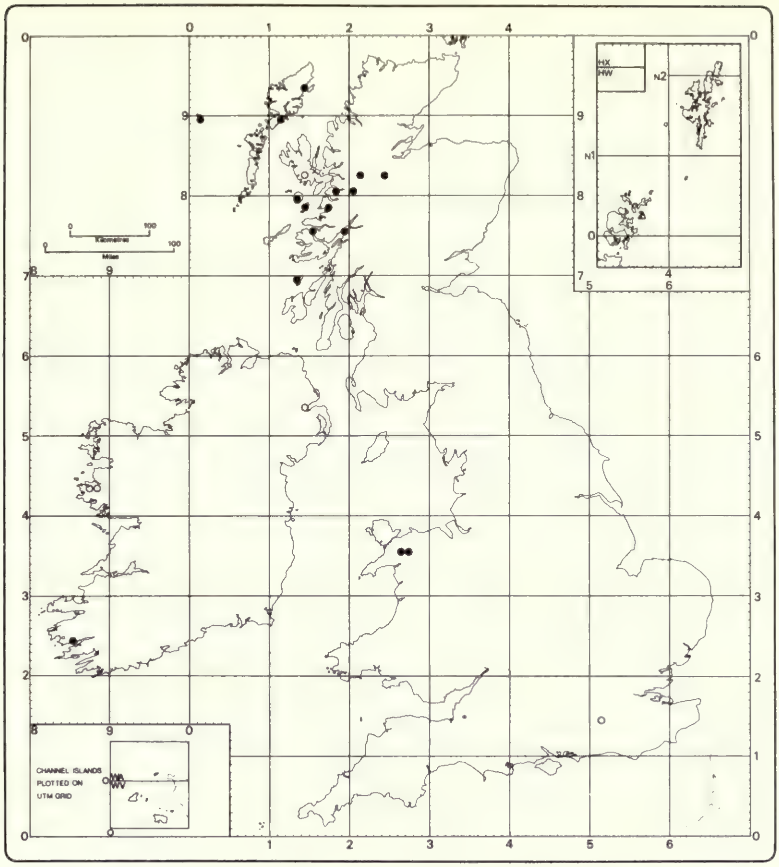
Lecidea milliaria var. *endoleuca* Leighton, *Lich. Fl. Brit.*, edn 3: 363 (1879). Type: Ireland, West Galway, on the Doughraugh, 1875, *C. Larbalestier* (BM ex K – lectotype!; BM – ? isolectotype!).

Thallus identical to var. *lignaria* except that the areolae usually have dull yellowish (isabelline) tinge.

Apothecia and *pycnidia* (containing microconidia) identical to var. *lignaria*; pycnidia containing macroconidia or mesoconidia not known.

Chemistry: Thallus K− or Kf+ yellow, C+ yellow-orange (persistent), KC+ reddish orange (persistent), PD−; sections of apothecia C−; t.l.c.: xanthone(s), possibly arthothelin and thiophaninic acid.

Observations (including *habitat and distribution*): My preliminary studies on *M. lignaria* found most specimens to have a C−, PD+ red thallus reaction, but a few otherwise ± identical specimens from western Ireland, north Wales, and western Scotland gave C+ persistent orange, PD− reactions. Subsequent t.l.c. analysis proved the normal form to have the then unidentified, P+ red compound found also in *Phyllopsora rosei* (Coppins & James, 1979), and the anomalous form to contain two xanthones (possibly arthothelin and thiophaninic acid). Xanthones often impart a yellowish tinge to lichen thalli (e.g. *Lecidella elaeochroma, L. scabra, Pertusaria flavida*, and *P. hymenea*) and this is the case for the xanthone containing race of *M. lignaria*; the colour difference is most evident when the two races occur together. Of all the types of names attributable to *M. lignaria s. ampl.*, only that applicable to the 'var. *endoleuca* Leighton' was found to contain xanthones, and that name is here adopted at the same rank. Although the var. *endoleuca* is morphologically identical to the var. *lignaria* it has a sympatric but much more restricted geographical range. In the British Isles it is confined to the more oceanic districts with one rather anomalous occurrence in Surrey (Leith Hill). Furthermore, it appears to have a lower altitudinal range, with a collection at 600 m in Snowdonia representing its known upper limit in



Map 10 *Micarea lignaria* var. *endoleuca* ● 1950 onwards ○ Before 1950

the British Isles. Only four examples of var. *endoleuca* have been discovered from outside Britain: from Baden (Heidelberg) and Bavaria (Bayreuth) in Germany, Bern (Langnau) in Switzerland, and Trentino (Appiano) in northern Italy. It should be checked for amongst material from other regions, especially south-west Norway, Bretagne (France) and the Pyrénées.

I believe that the var. *endoleuca* should be retained at varietal rank. However, as the depsidone argopsin (1′-chloropannarin) of var. *lignaria* is probably biogenetically distinct from the xanthones of var. *endoleuca*, a case could be made for its recognition at species rank. A comparative example is *Parmeliopsis ambigua* versus *P. hyperopta* (see Hawksworth, 1976).

20. **Micarea lithinella** (Nyl.) Hedl.
(Figs 4A, 20A–B; Map 11)

in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 78, 97 (1892). – *Lecidea lithinella* Nyl. in *Flora, Jena* **63**: 390 (1880). – *Lecidea lithinella* Nyl. in *Flora, Jena* **45**: 464 (1862); *nom. nudum* (Art. 32). Type: Germany, Bayern, 'Sandsteineblöcke am Waldwege von Banz nach Altenbanz in Oberfranken', ix 1860, *F. Arnold* 957 (M – lectotype!; H-NYL 19192 – isolectotype (fragment)!).

Thallus effuse, saxicolous, often a thin indistinct crust between protruding grains of rock, but somes developing irregularly rounded, convex, more rarely subglobose, whitish areolae, *c.* 40–100 μm diam. *Phycobiont* micareoid, cells 4–6·5 μm diam.

Apothecia numerous, immarginate, adnate, convex, apparently never tuberculate, pallid or dull yellow-orange to reddish brown (never black), (0·1–)0·15–0·4 mm diam. *Hymenium* 35–50 μm tall, hyaline but often tinged dilute straw in upper part. *Asci* cylindrical-clavate, 35–50×8–13 μm. *Spores* ovoid or fusiform-ellipsoid, simple, 6·5–9·5×2·8–4 μm. *Paraphyses* scanty, simple or irregularly forked above, 0·7–1 μm wide but sometimes gradually widening towards the apices and up to 1·5 μm wide, hyaline throughout. *Hypothecium c.* 50–70 μm tall, yellow-straw to dilute orange-brown, K−, HNO_3−, pigment confined to gel-matrix and hyphal walls hyaline. *Excipulum* absent (not detected even in sections of young apothecia).

Pycnidia apparently rare, very inconspicuous, immersed, *c.* 40 μm diam, with hyaline walls. *Conidia* (*microconidia*) narrowly cylindrical, 4–5·7×0·8–1 μm.

Chemistry: Thallus C−, K−, PD−; section of apothecia C−; t.l.c.: not tested.

Observations: M. lithinella exhibits little variation except that between, and sometimes within, collections there is an intergradation from pallid apothecia with a dull yellowish hypothecium to darker apothecia with an orange-brown hypothecium. This variation is correlated with differences in exposure to light. *M. lithinella* is easily confused with forms of *M. bauschiana* with pallid apothecia. Difficult specimens can be determined by a careful examination of the phycobiont, which is micareoid in *M. lithinella* but non-micareoid (cells *c.* 7–13 μm diam) in *M. bauschiana. M. lutulata* has darker apothecia which are commonly tuberculate, a darker (opaque) hypothecium, an often greenish hymenium, and non-micareoid phycobiont. *M. muhrii* is normally lignicolous but has once been found on rocks; it has adnate apothecia like *M. lithinella* but they are usually darker and have a taller, dark reddish brown hypothecium, and usually a greenish upper hymenium. *M. myriocarpa* shares a similarly coloured hypothecium with *M. lithinella*, but has smaller, globose to tuberculate apothecia and smaller, 1-septate spores.

In their keys to *Micarea* Vězda & Wirth (1976) and Poelt & Vězda (1977) state that *M. lithinella* has a K+ violet hymenium and often 1-septate spores; this is clearly an error, probably due to confusion with saxicolous forms of *M. denigrata* or *M. prasina*.

Habitat and distribution: M. lithinella occurs on acidic rocks, especially hard sandstone. Associated species encountered on the specimens examined include *Baeomyces rufus* (parasitized by *Thelocarpon lichenicola* on the lectotype of *Lecidea lithinella*), *Huilia crustulata Rhizocarpon obscuratum, Scoliciosporum umbrinum, Trapelia coarctata,* and *T.* aff. *obtegens.* This list of associates, plus information on some of the packets, suggest that *M. lithinella* has mostly been found in humid situations on outcrops and boulders by woodland roads. It was collected by Arnold, Lahm and von Zwackh from several areas of Germany: Bayern, Nordrhein-Westfalen and Baden-Württemberg, respectively. In Sweden it was collected in Uppland by Hedlund who (1892: 97) also cited a collection by Blomberg from Södermanland. One British specimen has recently been found: South-east York (V.C. 61), Wharram Quarry Nature Reserve, 44/85. 65, 1969, *Coppins* (E). At this locality *M. lithinella* was growing with *Scoliciosporum umbrinum* on the underside of a large flint; the upper, more exposed, part of the flint was colonized by *Lecidea erratica* and *Rhizocarpon obscuratum*.

Exsiccata: Arnold *Lich. Exs.* 836 (BM ex K, H-NYL 19190, M). Lojka *Lich. Univ.* 233 (M). Malme *Lich. Suec.* 125 (M, S). Zwackh *Lich. Exs.* 590 (H-NYL p.m. 5404, M).

21. **Micarea lutulata** (Nyl.) Coppins
(Figs 20C, 44B; Map 11)

in D. Hawksw., P. James, & Coppins in *Lichenologist* **12**: 107 (1980). – *Lecidea lutulata* Nyl. in *Flora, Jena* **56**: 297 (1873). Type: Jersey, Rozel meadow, bases of rocks, 1873, *C. Larbalestier* (H-NYL 10696 – lectotype!; BM – isolectotype!; M – probable isolectotype!). See note below.

Lecidea laxula Nyl. in *Flora, Jena* **58**: 11 (1875). Type: Finland, Tavastia australis, Luhanka, Hietala, 1874, *E. A. Lang [Vainio]* 303 (H-NYL 20689 – lectotype!; H – isolectotype!).

Lecidea poliodes Nyl. in *Flora, Jena* **58**: 10 (1875). – *Micarea poliodes* (Nyl.) Vězda *in* Vězda & V. Wirth in *Folia geobot. phytotax., Praha* **11**: 99 (1976). Type: Finland, Tavastia australis, Evo, [on schistose rock with *M. sylvicola*], *J. P. Norrlin* (H-NYL 20683 – holotype!).

Lecidea antrophila Larb. ex Leighton in *Trans. Linn. Soc. London* (Bot.) II, **1**: 242 (1876). Type: Ireland, West Galway, Mwellan near Kylemore, in the interior of a cave, 1877, *C. Larbalestier* (BM ex K – lectotype!; isolectotypes: BM!, BM ex K!).

Lecidea paucula Nyl. in *Flora, Jena* **59**: 573 (1876). Type: Ireland, West Galway, 'Montagnes de Maam' [Maumturk Mountains], iii 1876, *C. Larbalestier* (H-NYL 20090 – holotype!).

Micarea umbrosa Vězda & V. Wirth in *Folia geobot. phytotax., Praha* **11**: 93 (1976). Type: Germany, Baden, Südschwarzwald, between Neuhäusle and Altglashütte near St. Märgen, 830 m, 2 v 1969, *V. Wirth* (hb. Wirth 1609 – holotype!).

Lecidea granvina Vainio *in* Havaas in *Bergens Mus. Årb.* **1909** (1): 31 (1909); *nom. nudum* (Art. 32). Spec. orig.: Norway, Hordaland, Hardanger, Granvin, 10 xi 1900, *J. J. Havaas* (BG!).

Lecidea demarginata auct. p.p., non Nyl.; see 'Excluded Taxa'.

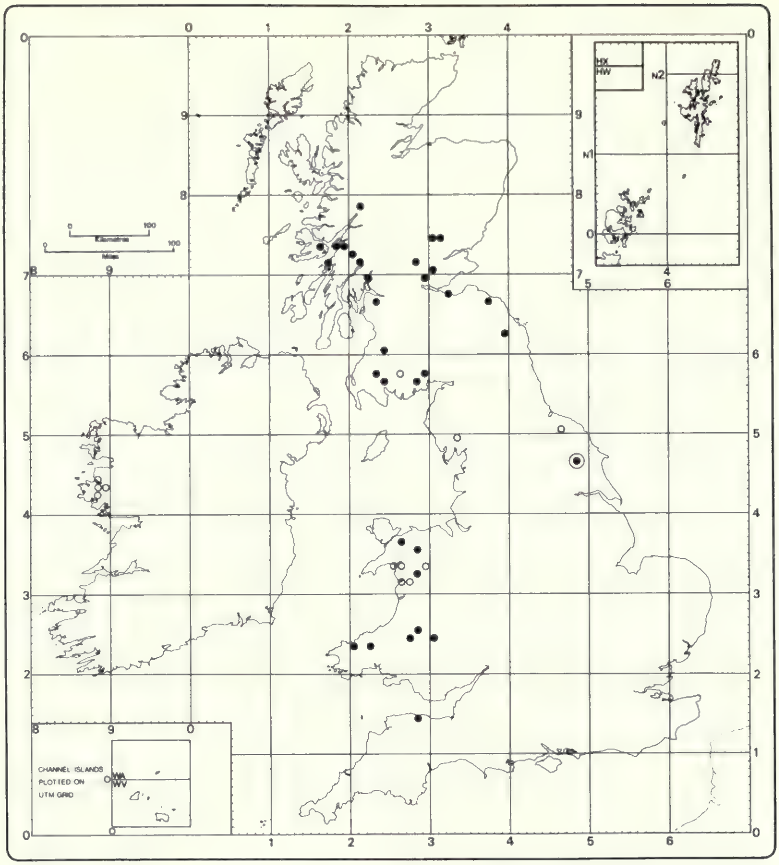
Note: typification of *Lecidea lutulata*. Larbalestier's gatherings in BM and H, that were collected from Rozel meadow in 1873 and subsequently labelled '*Lecidea lutulata*', consist of *M. bauschiana, M. lutulata* and *M. peliocarpa*. The specimen H-NYL 10696 contains *M. lutulata* only and agrees with the original diagnosis, e.g. 'hypothecium fusconigricans crassum', and is therefore selected as lectotype.

Thallus effuse, thin (up to 40 μm thick), ± smooth or finely rimose, usually becoming thicker (up to 600 μm thick) and scurfy-granular (but never forming discrete areolae or goniocysts), pale greenish grey or grey-green, sometimes straw-coloured in part, sometimes oxydated (on ferruginous rocks); in section ecorticate and without an amorphous hyaline covering layer. *Phycobiont* not micareoid; cells thin-walled, ± globose, *c.* 5–12 μm diam, or ellipsoid and up to 15×8 μm.

Apothecia numerous, convex-hemispherical and immarginate from the start, later becoming ± globose or tuberculate, grey-brown, dark brown or blackish, always turning blackish when moistened, 0·2–0·4 mm diam, or up to 0·8 mm diam when tuberculate. *Hymenium* 30–40 μm tall; upper part varying from hyaline or pale fuscous-brown through olivaceous to dark aeruginose, pigment often in patches corresponding to clustered apices of stout paraphyses, K−, HNO_3+ red; lower part hyaline or dilutely coloured. *Asci* cylindrical-clavate, *c.* 30–40×7–10 μm. *Spores* ellipsoid, ovoid, or sometimes dacryoid, 6–8(–9)×2–3(–3·4) μm. *Paraphyses* rather scanty, of two types: *p.p.* evenly distributed, irregularly flexuose, simple, or forked or with short branches (especially in the upper part), sometimes anastomosing, 0·8–1(–1·5) μm wide, apices sometimes irregularly swollen to *c.* 2 μm wide; *p.p.* fasciculate, mostly simple, stout, *c.* 1·5–2 μm wide, with swollen (to 3 μm), coherent, pigmented apices. *Hypothecium* 120–360 μm tall, dark and opaque, fuscous- or reddish brown, K− or + reddish intensifying (but never with purple or greenish tinges), HNO_3−; hyphae interwoven, but becoming vertically orientated towards the hymenium, *c.* 1·5–2 μm wide but coated with dense brown pigment and appearing 3–4 μm wide; ascogenous hyphae with swollen cells *c.* 2–4 μm wide. *Excipulum* not seen even in sections of young apothecia; the hymenium soon becomes reflexed so as to form an excipulum-like zone below the hypothecium. *Pycnidia* often present but inconspicuous, immersed, blackish, *c.* 80–200 μm diam, ostiole often gaping; with a single ± globose locule but walls often convoluted with up to 5 locules seen in a vertical section; outer walls reddish brown, K−; inner walls of secondary locules hyaline; *conidiogenous cells* irregularly cylindrical, often with 1–2 percurrent proliferations, 7–10×1–1·5 μm, base sometimes swollen to 2·7 μm wide; *conidia* (*mesoconidia*) cylindrical, sometimes faintly biguttulate but not constricted in the middle, (3·8–)4–5(–5·5)×0·9–1·4 μm.

Chemistry: All parts K−, C−, PD−; t.l.c.: no substances detected.

Observations: The apothecia of *M. lutulata* have a similar internal pigmentation to those of *M. botryoides* (*q.v.*) and *M. muhrii* (*q.v.*), but the species is most often confused with *M. sylvicola*. The latter shares the same habitat as *M. lutulata*, but can be distinguished by its hypothecium which always has a distinctly green, or rarely purplish, tinge in water mounts or KOH; in HNO_3 the pigment(s) turn purple-red. *M. sylvicola* further differs in its larger spores, taller hymenium, slightly longer and broader conidia, and presence of greenish pigment in its pycnidial walls. *M. myriocarpa* occurs in similar habitats to *M. lutulata* and has a reddish brown, but never opaque (in thin section) hypothecium. Furthermore, *M. myriocarpa* has smaller apothecia, narrower, often 1-septate spores, and sessile pycnidia with much shorter conidia.



Map 11 *Micarea lithinella* ◉ 1950 onwards + *Micarea lutulata* ● 1950 onwards ○ Before 1950

Habitat and distribution: M. lutulata is found on rocks and sometimes exposed roots in dry rocky underhangs, and is a characteristic species of the *Micareetum sylvicolae*. It is apparently widespread in northern and western Britain; and although not yet reported from the south-west peninsula of England or the north-west of Scotland, it almost certainly occurs in those areas. It appears to be little known outside of the British Isles, but I have seen material from Norway (Oppland and Hordaland), Sweden (Värmland), southern Finland, Germany (Baden-Württemberg), and Czechoslovakia (Bohemia: Krkonoše).

Exsiccata: Arnold *Lich. Exs.* 409B *p.p.* (WRSL). Havaas *Lich. Exs. Norv.* 571 (BG). Larbal. *Lich. Herb.* 223 (BM, BM ex K). Räsänen *Lich. Fenn.* 672 *p. p.* (LD-mixed with *M. tuberculata*).

22. **Micarea melaena** (Nyl.) Hedl.
(Figs 21A, 46A; Map 12)

in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 82, 96 (1892). – *Lecidea melaena* Nyl. in *Bot. Notiser* **1853**: 182 (1853). – *Lecidea vernalis* var. *melaena* (Nyl.) Nyl. in *Mém. Soc. Imp. Sci. nat. Cherbourg.* **3**: 182 (1855). – *Bacidia melaena* (Nyl.) Zahlbr. in *Annls mycol.* **7**: 474 (1909). Type: Sweden, on lignum, *E. M. Fries, Lich. Suec. Exs.* 212B (UPS – lectotype!; isolectotypes: C!, H-NYL p.m. 4778 [fragment]!, M!).

Lecidea milliaria var. *turfosa* Fr., *Nov. Sched. Crit.* **8**: 7 (1826), non *Biatora turfosa* Massal. Type: Sweden, [? Småland], on peaty turf, *E. M. Fries, Lich. Suec. Exs.* 212A (UPS – lectotype!; isolectotypes: C!, M!).

Biatora stizenbergeri Hepp, *Flecht. Eur.* no. 504 (1860). Type: Switzerland, Rifferschweil, on dry plant debris amongst roots in peat moor, *Hegetschweiler* (BM – lectotype!; isotypes distributed in Hepp. Flecht. Eur. 504: BM!, E!, WRSL!).

Lecidea ilyophora Stirton in *Scott. Nat.* **5**: 220 (1879). Type: Scotland, Perthshire, Black Wood of Rannoch, on lignum, ix 1879, *J. Stirton* BM – lectotype! [t.l.c.: no substances detected]).

Lecidea melaena f. *catillarioides* Vainio in *Medd. Soc. Fauna Fl. fenn.* **10**: 12 (1883). – *Micarea melaena* f. *catillarioides* (Vainio) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 83, 96 (1892). Type: Finland, Karelia borealis, Nurmes, Riihivaara, on bryophytes on rock, 1875, *Vainio* (TUR-VAINIO 21478 – holotype!).

Lecidea melaena f. *endocyanea* Vainio in *Medd. Soc. Fauna Fl. fenn.* **10**: 12 (1883). – *Micarea melaena* f. *endocyanea* (Vainio) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III **18** (3): 83, 96 (1892). Type: USSR, Karelia keretina, Kivakka, on mosses on rocks, 1877, *Vainio* (TUR-VAINIO 21476 – holotype!).

Bilimbia melaena f. *aeruginosa* Vainio in *Acta Soc. Fauna Fl. fenn.* **53** (1): 254 (1922). Type: Finland, Tavastia australis, Hollola, on lignum, 1875, *Vainio* (TUR-VAINIO 21461 – lectotype!).

Bilimbia melaena f. *epiphaeotera* Vainio in *Acta Soc. Fauna Fl. Fenn.* **53** (1): 255 (1922). Type: Finland, Karelia borealis, Nurmes, Louhivaara, 'Kallion syrjällä', on bryophytes and old *Cladonia* squamules, 1875, *Vainio* (TUR-VAINIO 21472 – lectotype!).

?*Bilimbia melaena* var. *alnicola* Savicz in *Izv. imp. S. Peterb. bot. Sada* **14** (I, Suppl.): 53 (1914). Type: USSR (?LE); request for loan received no reply.

Bilimbia milliaria γ. [var.] *saprophila* Körber, *Parerg. lich.*: 171 (1860); *nom. superfl.* (Art. 63).

Thallus effuse, superficial, of small, scattered to coherent or clustered, granular areolae (20–)25–80(–100) µm diam, sometimes forming an uneven crust up to *c.* 150 µm thick. Areolae very variable in colour, pale buff or pale dull green to dark grey-green; in section without an amorphous covering layer, outermost hyphae often with dark green (K−, HNO_3+ red) walls. Thallus often scurfy granular and blackish (especially in damp situations) owing to its disruption by invading dematiaceous fungi and foreign algae; in dry situations (e.g. undersides of fallen trunks) it may have a whitish or pale yellowish, farinose appearance due to a thick covering of an epiphytic alga, each cell of which is coated by hyaline, crystalline incrustations. *Phycobiont* micareoid, cells *c.* 4–7 µm diam.

Apothecia numerous, immarginate, convex-hemispherical to ± globose, sometimes tuberculate, black, matt or slightly glossy, 0·12–0·4 mm diam, or to 0·5 mm diam when tuberculate. *Hymenium* 30–40(–50) µm tall, dull to bright aeruginose or grey-blue, K− or K+ green intensifying; alternatively lower part (or rarely the entire hymenium) dilute purple-brown, K+ greenish or K+ purple intensifying; pigment(s) often more dense around the apices of the paraphyses, thus appearing as a dark 'epithecium' (*c.* 2–10 µm tall) that contrasts with the more dilute colouration of the rest of the hymenium. *Asci* clavate, *c.* 30–40–12–15 µm. *Spores* ovoid-oblong or oblong, with rounded apices, straight, (1–)3(–5)-septate, 12–21×4–5(–5·5) µm. *Paraphyses* numerous, branched and anastomosing, sometimes a few unbranched, thin, 0·8–1 µm wide; apices not swollen, or sometimes slightly incrassate and up to 1·5 µm wide, hyaline but often individually surrounded by a pigmented hood of dense gel (easily detached in mounts in K, by tapping the cover slip). Occasionally intermixed with ordinary paraphyses are a few which are simple, stout (*c.* 1·5–2 µm wide) and coated with pigment throughout their length so as to appear 3–4 wide. *Hypothecium c.* 80–160 µm tall, dark and ± black in thick sections, pigmentation variable (see 'observations' below), usually purple-brown and K− or K+ purple intensifying, or, outer (more rarely whole) part K+ olivaceous with central part ('core') remaining ± purplish brown; all parts HNO_3+ purple-red; hyphae *c.* 0·7–1·5 µm wide but their walls coated with dense pigment so that they appear to be *c.* 3–4 µm wide, interwoven or becoming vertically orientated towards the hymenium, sometimes a few extending into the hymenium as stout pigmented paraphyses; ascogenous hyphae similarly pigment, short-celled, *c.* 2–5 µm wide. *Excipulum* indistinct, sometimes evident in sections of young apothecia, green or purplish (usually darker than hymenium, but paler than hypothecium); hyphae radiating, branched and anastomosing, *c.* 0·7–1 µm wide.

Pycnidia rare, black, of two types: (a) *c.* 100–140 µm diam, sessile; walls purple-brown or dull olive, K+ green; *conidia* (*macroconidia*) curved or hamate, 0–7-septate, 18–33×1–1·5 µm; (b) *c.* 40–60 μm diam, semi-immersed to sessile, walls green, K−; *conidia* (*microconidia*) fusiform-cylindrical, straight, 4·8–7×0·8–1 μm.

Chemistry: Thallus K−, C+ red or C−, PD; sections of apothecia C−; t.l.c.: gyrophoric acid (healthy thalli), or no substances or gyrophoric acid in trace amounts (poorly developed or disrupted thalli).

Observations: Micarea melaena is one of the commonest species of the genus, especially in northern Europe, and it displays a considerable amount of variation in thallus appearance and internal apothecial pigmentation. However, my examinations of over 200 specimens have revealed many intermediates between the known extremes. When well-developed, the thallus is composed of cohering, small, granular areolae and is pale buff to dull green in colour. In exposed situations the thallus often becomes a dark green-black due to the more intense pigmentation of the outermost hyphae of the granules. The appearance of the thallus can also be affected by the presence of other organisms (see description and p. 00). When on lignum, in dry exposed situations the thallus may become much reduced to a fine scattering of tiny (less than 30 μm diam), blackish granules amongst the wood fibres. Such forms proved to be very common, during my explorations in Sweden.

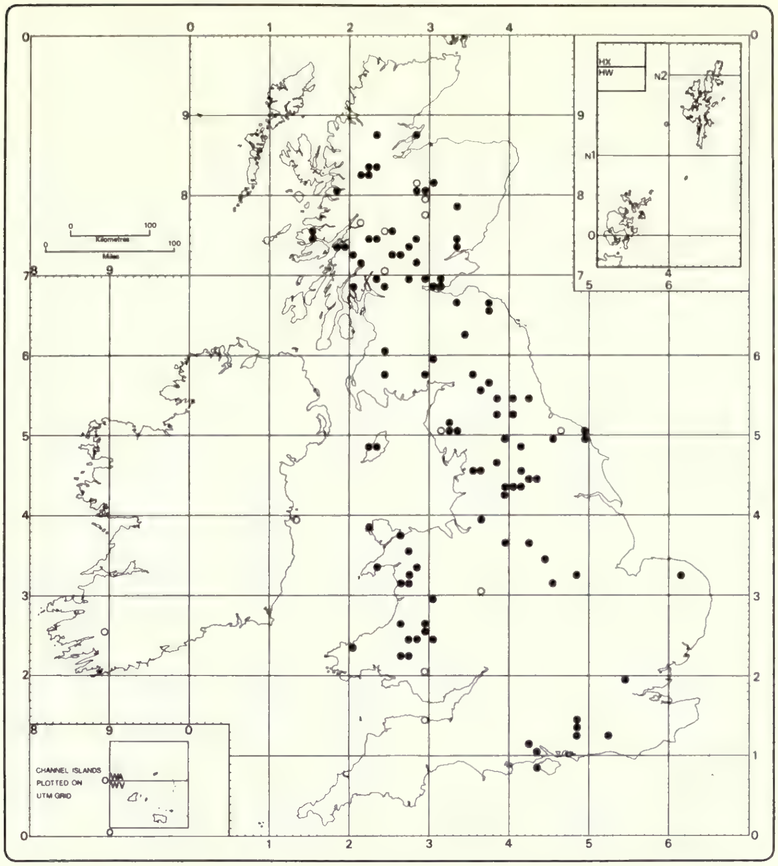
M. melaena also exhibits much variation with regard to the colouration of its apothecial tissues (especially the hypothecium). This is due to the presence of three (probably biosynthetically related) pigments, varying in their relative amounts and distribution. These pigments, all of which react HNO_3+ purple-red, can be roughly identified as pigment A: green, K+ green intensifying; pigment B: purple, K+ green; pigment C: purple, K+ purple intensifying.

In the epithecium and hymenium pigment A is often found alone, but sometimes it is replaced in the lower hymenium (or in extreme cases throughout the entire hymenium and epithecium) by pigment C. Pigment C is usually dominant in the hypothecium, but is often replaced in the upper and outer parts (or more rarely ± throughout) by pigment B. If thin sections of apothecia in which pigment B is dominant are mounted in K the lower central ('core') of the hypothecium retains a purplish tinge (the rest having turned green), indicating the presence of a small amount of pigment C. The same type of variation, presumably involving identical (or very similar) pigments, is found in several other species, e.g. *M. crassipes* and *M. sylvicola*.

The pycnidia of *M. melaena* are very inconspicuous and apparently sparingly produced. However, a close scrutiny of about 100 specimens revealed ten collections with the microconidial state and only two (e.g. Coppins 6041) with the macroconidial state. A mesoconidial state was not found but may well occur.

Habitat and distribution: M. melaena is widely distributed and especially common in north-west Europe. Although, for a *Micarea*, it is a conspicuous species, it is often overlooked as a black or charred stain on the tops of stumps and peaty turf! It is a common inhabitant of stumps and fallen decorticate trunks in upland woodlands, or in lowland woodlands on very acid, nutrient-poor soils, and can exist in shaded to extremely exposed, sun-baked situations. In upland woods it can be found on the corticate trunks of healthy trees (especially *Betula, Quercus*, and *Pinus*). In areas heavily polluted by SO_2 and its derivatives (e.g. West Yorkshire conurbation) it has been found on the acidified bark of *Acer* and *Ulmus*. Occurrences on decaying timber work (e.g. fence posts, gate rails and shingles) are not uncommon, especially in upland districts. Lichens associated with *M. melaena* on lignum and bark in the British Isles include *Bryoria capillaris, B. fuscescens, Cladonia* spp., *Hypocenomyce scalaris, Hypogymnia physodes, Lecidea granulosa* agg., *L. icmalea, Micarea denigrata, M. prasina, Mycoblastus sterilis, Ochrolechia turneri, Parmelia saxatilis, Parmeliopsis* spp., *Platismatia glauca, Trapelia corticola*, and *Usnea* spp.

M. melaena is often terricolous, growing on oligotrophic, peaty soils, in montane regions or lowland heaths. In the English lowlands it is recorded from heaths in the Sussex Weald and east Norfolk. It is common on ± bare peat in the Pennines and Scottish highlands, but in the latter it is usually replaced near the higher summits (over *c.* 1000 m) by *M. turfosa*. Associated lichens on peaty turf in Britain include *'Botrydina'* (i.e. *Omphalina* spp.), *Cladonia coccifera, C. crispata,*



Map 12 *Micarea melaena* ● 1950 onwards ○ Before 1950

C. floerkeana, C. subcervicornis, Coelocaulon aculeatum s. lat., *Lecidea icmalea, Micarea leprosula,* and *Ochrolechia androgyna. M. melaena* is often found on rocks, growing over peaty debris or decaying mats of bryophytes and *Cladonia* squamules, but occurrences where it is growing directly on rock are rare. To my knowledge, all such occurrences in Britain are confined to woodland situations in rather heavily polluted areas approximating to zones 3–5 on the scale of Hawksworth & Rose (1970); these areas include Leicestershire, the West Yorkshire conurbation, and Fife.

M. melaena is widely distributed in mainland Britain, but is particularly common in the upland areas of the north and west. There is a dearth of records from Ireland, where it is unlikely to be rare in suitable terrain. *M. melaena* is known from most parts of the European mainland and is particularly common in the boreal regions of Fennoscandia and upper Bavaria and adjoining alpine districts, but this apparent tendency may, at least partially, be a reflection of the avidity of the collectors active in those areas, and the herbaria which I have studied! It has been found in the Azores on *Cryptomeria* and sulphur-rich soils near fumaroles, but it is so far unrecorded from the Canary Islands. From outside Europe I have seen several collections from eastern Canada and north-eastern U.S.A.

Exsiccata: Anzi Lich. Exs. Ital. 259A (BM, M). Anzi *Lich. Sondr.* 170B (UPS). Arnold *Lich. Exs.* 332A–C (M). Arnold *Lich. Mon.* 49 (M), 248 (C, M), 249 (C, MANCH), 407 (C, M, MANCH). Britz. *Lich. Exs.* 946 (M). Fellman *Lich. Arct.* 159 (H). Flotow *Lich. Exs.* 129C (UPS). Fries *Lich. Suec.* 212A, B (C, H-NYL p.m. 4778, M, UPS). Hepp *Fl. Eur.* 504 (BM, E, WRSL). Johnson *Lich. Herb.* 376 (BM). *Krypt. Exs. Vindob.* 362 (BM, M). Leighton *Lich. Brit.* 120 (BM). Malme *Lich. Suec.* 27 (C, M, S). Moug.

& Nestl. *Stirp. Crypt.* 1329 *p.p.* (E). Mudd *Lich. Brit.* 159 (M, MANCH). Norrlin & Nyl. *Herb. Lich. Fenn.* 180 (BM, C, M). Oliv. *Lich. Orne* 237 (M). Räsänen *Lich. Fenn.* 963 (M). Räsänen *Lichenoth. Fenn.* 344 (BM). Roum. *Lich. Gall.* 231 (M). Schaerer *Lich. Helv.* 196 *p.p.* (E). Vězda *Lich. Sel.* 14 (BM, M). Zwackh *Lich. Exs.* 657, 675 (M).

23. **Micarea melaenida** (Nyl.) Coppins, **comb. nov.**
(Fig. 22)

Lecidea melaenida Nyl. in *Flora, Jena* **48**: 146 (1865). – *Catillaria melaenida* (Nyl.) Arnold in *Flora, Jena* **53**: 475 (1870). Type: France, [? Eure], Perrières, *Lenormand* (H-NYL 18843 – holotype!).

Lecidea relicta Nyl. in *Flora, Jena* **48**: 354 (1865) [nec Stirton (1876)]. Type: France, Calvados, Falaise, *L.-A. De Brébisson* (H-NYL 21099 – holotype!).

Catillaria schumannii ['*Schumanni*'] Stein *in* Cohn, *Krypt. -Fl. Schles.* **2** (2): 232 (1879). – *Lecidea schumanni* Körber, *Syst. Lich. Germ.*: 255 (1855); *nom. inval.* (Art. 34). Type: East Germany, Reichenbach, near Ernsdorf, *Schumann* (WRSL – lectotype!; WRSL – isolectotype!).

Catillaria zsakii Szat. in *Magy. bot. Lap.* **24**: 108 (1926). – *Toninia zsakii* (Szat.) Lettau in *Feddes Reprium Spec. nov. veg.* **57**: 9 (1955). Type: holotype not seen (? in BP); topotypes: Hungary, 'In argillosis natronatis prope oppidum Karcag, Comit. Jász-Nagykun-Szolnok. Allit. ca. 80 m. s.m. Mens. Szept. 1926', *Z. Zsák & G. Timkó, Fl. Hung. Exs.* 714 (E! [t.l.c.: no substances], BM!, BM ex K!), and, from same locality but at '100 m. s.m.' and no date, *Krypt. Exs. Vindob.* 3154 (BM!, BM ex K!).

Catillaria schumanni var. *meridionalis* Roux & Vězda *in* Vězda, *Sched. Lich. Sel. Exs.* 537 (1967). Type: France, Gard, Pujaut near Avignon, alt. 100 m, 'supra solum argillaceo-sabulosum, ad marginem Querceti ilicis', 6 xi 1966, *C. Roux,* Vězda *Lich. Sel. Exs.* 537 (BM – isotype!).

Thallus effuse, terricolous (on argillaceous soils), forming a thin ± smooth, dull greenish white crust, *c.* 40–100 μm thick, or forming confluent, convex areolae 0·1–0·6 mm diam; crust sometimes becoming cracked so as to appear ± 'squamulose'. Thallus in section without a distinct hyaline, amorphous, covering layer, but with a hyaline 'cortex' 12–20 μm tall, composed of compacted, evacuated hyphae (cytoplasm presumed lost owing to lack of staining by LCB or ammoniacal erythrosin); thallus hyphae 1·5–2·5(–3) μm wide; numerous algae-free hyphae penetrating the soil substratum to a depth of *c.* 1 mm (? or more). *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia numerous, scattered or 2–4-confluent, immarginate, convex to hemispherical, black, matt, 0·2–0·6 mm diam; old, contorted apothecia sometimes reaching 1·2 mm diam; occasionally a fine weft of radiating, white (hyaline) hyphae is seen around the edge of an apothecium. *Hymenium* 35–40 μm tall; uppermost *c.* 1–5 μm (epithecium) with dense, amorphous, purple-brown pigment, K−, HNO_3+ purple-red; remaining (lower) parts dilute dull purple, K−, HNO_3+ red. *Asci* clavate, 35–38×9–12 μm. *Spores* ellipsoid, oblong-ellipsoid or ovoid-oblong, straight or slightly curved, 0–1-septate, (7–)9·5–15×3–4(–4·5) μm. *Paraphyses* numerous, mostly simple below, but often branched above, sometimes anastomosing, 1–1·7 μm wide; apices (upper 5–15 μm) often purple-brown pigmented and to 2·5 μm wide. *Hypothecium* 60–120(–200) μm tall, mottled dark purplish brown, K−, or K+ purple intensifying in part, HNO_3+ purple-red; hyphae interwoven but ± vertically orientated in uppermost part, *c.* 1–1·8 μm wide, each with a densely pigmented gel sheath thereby giving a total diameter of *c.* 3 μm; ascogenous hyphae *c.* 2·5–5 μm wide. *Excipulum* soon reflexed, but distinct in sections of young apothecia, purple-brown (usually darker than hymenium); hyphae radiating, branched and anastomosing, *c.* 1·3–2 μm wide, embedded in densely pigmented gel-matrix.

Pycnidia often present, immersed, black, *c.* 50–100 μm diam; walls purple-brown, K− or Kf+ purple intensifying; *conidia* (? *microconidia*), ± cylindrical, 4·8–6(–7)×1 μm.

Chemistry: Thallus K−, C−, KC−, PD−; t.l.c.: no substances.

Observations: Micarea melaenida is characterized by its whitish, terricolous thallus, immarginate, black apothecia (with purplish pigmentation in section), numerous and rather stout paraphyses, and 0–1-septate spores. It is apparently related to *M. assimilata* (*q.v.*) and its allies. When compared with *M. melaenida*, forms of *M. melaena* with immature spores can be distinguished by their finely granular areolae, narrow and less numerous paraphyses, and usual presence of green pigments in apothecial sections (in water or K mounts). *M. turfosa* is similar in some ways to *M. melaenida*, but has a dark coloured thallus, an olivaceous hymenium, reddish brown (never purplish) hypothecium, and larger spores which are often 1–3-septate.

Habitat and distribution: M. melaenida grows on, and in direct contact with, fine-grained sandy or argillaceous, mineral soils, and is not known to occur on decaying bryophytes or plant debris, etc. Unfortunately I have never seen *M. melaenida* in the field, and there is little ecological information to be gleaned from the literature or herbarium labels. Furthermore, the specimens examined have included few associated species, and only *Cladonia* sp. (squamules) and *Catapyrenium lachneum* have been noted. In its Hungarian locality it was said to have occurred on soil rich in precipitated salts ('argillosis natronalis') although no effervescence was apparent when I tested the soil with 50% HNO_3. It is probable that *M. melaenida* is restricted to niches where the salts have been permanently leached out. A sample of soil from *Fl. Hung. Exs.* 714 was sent for analysis to the Macaulay Institute for Soil Research (Aberdeen) and Dr B. W. Bache of the Institute reports 'It bears no relationship at all to a sodic soil, and is in fact fairly acid, with pH 5·2. The conductivity is fairly low (0·8 mS in 1:2 extract), so it does not contain any great concentration of soluble salts, nor does it contain any carbonate.'

The data on the herbarium labels, although limited, do indicate that it occurs at low altitudes, for example the collection from Loire Atlantiqué was made from soil on coastal cliffs; that from Gard was made at 100 m; and those from Hungary were made at 80–100 m.

M. melaenida is a rare species with a rather southern distribution, and I have seen material from several localities in France (e.g. Loire Atlantiqué, Vienne, and Gard), and single localities in East Germany (Dresden) and Hungary. It is not known from Scandinavia, and its status as a British plant is doubtful. Its first British report seems to be its appearance in the checklist of James (1965*a*), but I have been unable to ascertain the reason for its inclusion. However, its presence in north-west France suggests that it could occur in Britain, especially along the south coast of England or in the Channel Islands.

Material from South Africa and distributed as Almborn *Lich. Africani* no. 84 is not *M. melaenida* but a mixture of two, undescribed species, both of which are probably referable to *Micarea*.

Exsiccata: Fl. Hung. Exs. 714 (BM, BM ex K, E). *Krypt. Exs. Vindob.* 3154 (BM, BM ex K). Vězda *Lich. Sel.* 537 (BM).

24. **Micarea melaeniza** Hedl.
(Figs 21B, 38B)

in *Bih. K. svenska VetenskAkad. Hand.* III, **18** (3): 83, 96 (1892). – *Lecidea melaeniza* ['*melaniza*'] (Hedl.) Zahlbr., *Cat. lich. univ.* **3**: 798 (1925). Type: Sweden, Hälsingland, lignum of old pine trunk, viii 1891, *J. T. Hedlund* (S – holotype!).

Thallus effuse, lignicolous (sometimes extending on to bryophyte or lichen thalli), endoxylic, or epixylic with whitish convex areolae; areolae *c.* 100–400 μm diam and up to 45 μm thick, without an amorphous covering layer. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia numerous, few, or absent, immarginate, at first convex-hemispherical or subglobose, often becoming tuberculate, black, matt, 0·2–0·3 mm diam, or to 0·5 mm diam when tuberculate. *Hymenium* 28–42 μm tall, upper and lower parts aeruginose-green, middle part ± hyaline with aeruginose vertical streaks; K– or dulling, HNO_3+ red. *Asci* clavate, 26–35×10–12 μm. *Spores* ovoid or dacryoid, simple, 5–9×2·5–3·8 μm. *Paraphyses* rather numerous, of two types; *p.p.* evenly distributed, flexuose, branched, thin, *c.* 0·7–1 μm wide, hyaline, but apices sometimes pigmented and then to 2·5 μm wide; *p.p.* scattered or in small fascicles, stout, *c.* 2 μm wide, each coated ± throughout their length by greenish pigment. *Hypothecium c.* 120–200 μm tall, dark brown, sometimes with a faint reddish (never purplish) tinge, K– or dulling, HNO_3– or red tinge slightly intensifying; hyphae coated with dark brown pigment and *c.* 2–3 μm wide, interwoven but becoming vertically orientated towards the hymenium and sometimes continuing into it as stout pigmented paraphyses; ascogenous hyphae similarly pigmented, but with short swollen cells to 5 μm wide. *Excipulum* not evident in available material.

Pycnidia numerous, black, sessile and *c.* 40–60 μm diam, or more usually borne on black stalks (pycnidiophores) and 80–300×40–70 μm (including stalk); stalks simple, or sometimes branched and bearing up to four pycnidia; upper part (pycnidial wall) dark olive but lower part (stalk tissue) reddish brown, both parts K−, *Conidia* (*mesoconidia*) short cylindrical, 2·3–3·6×1–1·3 μm

Chemistry: Thallus PD−; sections of apothecia and thallus C−; material insufficient for analysis by t.l.c.

Observations: With its black, subglobose to tuberculate apothecia, black, stalked pycnidia, inconspicuous thallus, and occurrence on lignum, *M. melaeniza* is indistinguishable in external appearance from *M. misella* and *M. nigella*. Microscopically, *M. misella* can be distinguished by the olivaceous (K+ violet) pigment in its hymenium and pycnidia, and its ± hyaline hypothecium; and *M. nigra* can be distinguished by the purple-brown (K+ green, HNO_3+ purple-red) pigment in its hymenium, hypothecium and pycnidia. With respect to apothecial and pycnidial pigmentation and structure, *M. melaeniza* is almost identical to *M. botryoides*. However, *M. botryoides* is rarely lignicolous, and has larger, often septate spores, and longer mesoconidia. *M. muhrii* has similar apothecial pigments to those of *M. melaeniza*, but is readily distinguished by its larger, adnate apothecia (which often have a pale marginal rim), larger spores, well developed excipulum, and lack of stalked pycnidia.

Habitat and distribution: M. melaeniza is a rare species, known only from three collections made in Sweden (Ångermanland, Hälsingland, and Småland) where it occurred on the lignum of conifer trunks. Associated species identified on the examined collections include *Calicium salicinum, Cetraria pinastri, Chaenothecopsis lignicola, Cladonia* spp. (squamules), *Dimerella diluta, Hypogymnia physodes, Lecanora symmicta* agg., *Micarea anterior, M. misella, M. prasina, Usnea* sp., and *Lophozia* sp.

25. **Micarea melanobola** (Nyl.) Coppins, **comb. nov.**
(Figs 21C, 46B–C)

Lecidea melanobola Nyl. in *Flora, Jena* **50**: 371 (1867). – *Catillaria melanobola* (Nyl.) Vainio in *Acta Soc. Fauna Fl. fenn.* **57** (2): 465 (1934). – *Lecidea erysiboides* **L. melanobola* (Nyl.) Nyl. *in* Hue in *Revue Bot. Courrensan* **5**: 103 (1886). – *Catillaria* β. *byssacea* f. *melanobola* (Nyl.) Blomb. & Forss., *Enum. Pl. Scand.*: 91 (1880). – *Micarea prasina* f. *melanobola* Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 87 (1892). Type: Finland, Tavastia australis, Kuhmois [Kuhmoinen], on bark of *Picea abies*, 1866, *J. P. Norrlin* (H-NYL 21614 – lectotype!; isolectotypes: H-NYL p.m. 4504!, H!).

Thallus effuse, thin and indistinct, of scattered to ± coherent, minute olivaceous granules (goniocysts), *c.* 12–25 μm diam, which appear ± gelatinous when moist. Outermost hyphae of goniocysts with greenish, K+ violet walls. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia numerous, convex-hemispherical, immarginate, dark grey to black, 0·1–0·24 mm diam. *Hymenium* 30–35 μm tall, hyaline, but with a clearly delimited, dark green epithecium, K+ deep violet, C+ violet, HNO_3+ red; pigment closely bound to (? or also in) the apical walls of the paraphyses, and also present in the gel-matrix and apical walls of the asci. *Asci* clavate, 30–35×9–11 μm, upper wall(s) sometimes tinged with greenish, K+ violet pigment. *Spores* ellipsoid, ovoid, or oblong-ovoid, with obtuse apices, 0–1-septate, 7–9·7×2·5–3·3 μm. *Paraphyses* scanty, branched and anastomosing, thin, 0·5–1 μm wide; apices thickened with greenish (K+ violet) pigment and up to 1·7 μm wide, often overtopping the tops of the asci. *Hypothecium* 25–70 μm tall, hyaline or dilute dull yellowish. *Excipulum* indistinct, sometimes evident as a non-amyloid, narrow (*c.* 10–15 μm), reflexed zone of radiating, branched and anastomosing hyphae, 0·5–1 μm wide.

Pycnidia numerous but small and inconspicuous, sessile, black, with dark greenish (K+ violet) walls; of two types: (a) 40–50 μm diam; *conidia* (*mesoconidia*) cylindrical or ovoid-

Table 6 Diagnostic features for the separation of *Micarea melanobola, M. misella,* and *M. prasina.*

	prasina	*melanobola*	*misella*
Apothecia colour	pallid to dark grey rarely black	dark grey to black	black, rarely paler
Apothecia size (mm)	0·1–0·4	0·1–0·25	0·1–0·3
Location of epithecial pigment	gel-matrix	walls of paraphyses + gel-matrix	gel-matrix
Spore septation	0–1(–3)	0–1	0(–1)
Spore length (μm)	8–14(–17)	6·5–9·5	7–9·7
Spore breadth (μm)	2·3–4(–5)	2–3(–3·7)	2·5–3·3
Paraphyses	usually numerous	sparse	sparse
Mesoconidia (μm)	(3·5–)4–6×1·2–1·7	3·3–4·5×1–1·3	3·5–5×1–1·5(–1·7)
Microconidia (μm)	(5–)5·5–8×0·7–1	4–5·5×0·7–0·8	3·8–6×0·6–0·8
Pycnidia (meso-)	immersed to sessile	sessile	stalked
Thallus type	goniocyst	goniocyst	endoxylic or areolate
Chemistry (t.l.c.)	one of 3 unknowns, ?± gyrophoric acid in trace amounts	unknown, not tested	± gyrophoric acid
Substrata	various	conifer bark	mostly lignum, not known on bark

oblong, often biguttulate and slightly constricted in the middle, 3·3–4·5×1–1·3 μm; (b) 25–40 μm diam; *conidia* (*microconidia*) cylindrical or fusiform-cylindrical, 4–5·5×0·7–0·8 μm.

Chemistry: Thallus and sections of apothecia C− (not red), but olivaceous pigment reacting C+ violet; material insufficient for analysis by t.l.c.

Observations: Presumably on account of its finely granular thallus, greenish (K+ violet) epithecium and small, 1-septate spores, *M. melanobola* was considered to be a form of *M. prasina* by Hedlund (1892), and a synonym of *M. prasina* by Vězda & V. Wirth (1976). Hedlund also suggested a relationship to *M. misella*, and I find that in many respects it is closer to *M. misella* than to *M. prasina*. The three species are compared in Table 6; this does not include features common to all of them (e.g. presence of olivaceous, K+ violet pigment, and ± hyaline hypothecia). The single feature separating *M. melanobola* from *both* the other species is the presence of closely adhering pigment on (? or in) the apical walls of its paraphyses. To this it may be possible to add some aspects of chemistry, but unfortunately there is not sufficient available material of *M. melanobola* for analysis by t.l.c. The principal features separating *M. melanobola* from *M. misella* involve thallus type, spore septation, insertion of mesoconidia-containing pycnidia and substrata. Similarly, those for separating *M. melanobola* from *M. prasina* involve the sizes of apothecia and spores, density of paraphyses and, above all, size of microconidia.

In external appearance *M. melanobola* is almost indistinguishable from *M. synotheoides,* but the latter is easily identified by its acicular spores.

Habitat and distribution: M. melanobola is only known with certainty from the type locality in southern Finland where it occurred on the bark of *Picea*. On the type specimens *M. melanobola* is accompanied by a few scattered *Cladonia* squamules, some small lobes of *Hypogymnia physodes* and *Parmeliopsis ambigua*, and a few small patches of *Dimerella diluta,* a white *Lepraria* sp., and *Pertusaria* ? *pupillaris* (soralia K−, PD+ red). Further well documented gatherings are required to obtain a better understanding of the ecology of this species.

26. **Micarea misella** (Nyl.) Hedl.
(Fig. 23A; Map 13)

in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 78, 88 (1892). – *Lecidea anomala* f. *misella* Nyl., *Lich. Scand.*: 202 (1861). – *Lecidea misella* (Nyl.) Nyl. in *Not. Sällsk. Fauna Fl. fenn. Förh.* **8**: 177 (1866). Type: Finland, Nylandia, Helsingfors [Helsinki], 1858, *W. Nylander* (H – lectotype!).

*Lecidea resinae** [subsp.] *L. globularis* Nyl., *Lich. Scand.*: 213 (1861). – *Lecidea globularis* (Nyl.) Lamy in *Bull. Soc. bot. Fr.* **25**: 435 (1878). – *Micarea globularis* (Nyl.) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 78, 88 (1892). Type: Sweden, 'Arthonia turgida var. γ globifera Svecia 112°' (H-ACH 52 – holotype!).

Lecidea melanochroza Leighton ex Crombie in *J. Bot., Lond.* **9**: 178 (1871). Type: Scotland, Perthshire, near Loch Tummel, *J. M. Crombie* (BM – lectotype!; isolectotypes: BM ex K!, and distributed in Crombie *Lich. Brit. Exs.* 174 (BM!) [note: this example includes *M. prasina* and those in E and M contain *M. prasina* only]).

Lecidea misella f. *brasiliana* Vainio in *Acta Soc. Fauna Fl. fenn* **7** (2): 57 (1890). Type: Brazil, Minas Geraes, Carassa, 1400 m, on lignum, *Vainio, Lich. Brasil. Exs.* 1420 (BM ex K – lectotype!; M – isolectotype!).

Bilimbia melaena f. *decrustata Vainio* in *Acta Soc. Fauna Fl. fenn.* **53** (1): 255 (1922). Type: Finland, Tavastia australis, Hollola, 1871, *Vainio* (TUR-VAINIO 21480 – lectotype!).

Lecidea asserculorum sensu Th. Fr., *Lich. Scand.* **2**: 473 (1874), non Ach (1810). See note by Hedlund (1892: 89).

Thallus effuse, often wide-spreading, usually lignicolous and endoxylic, sometimes developing on the surface of the substratum as convex to irregularly subglobose, greenish white to greenish grey, ± contiguous granular-areolae, *c.* 60–120(–150) μm diam. Areolae in section, without a well defined cortex or hyaline amorphous covering layer, but outer 5–12 μm is often tinged with olivaceous-brown pigment (K+ violet); pigment confined to gel-matrix and not adhering to hyphal walls. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia numerous, few or absent, scattered to crowded and confluent, immarginate, convex-hemispherical to subglobose, sometimes shortly stipitate, sometimes tuberculate, black, rarely pallid or grey-brown (shade forms), matt. *c.* 0·1–0·3 mm diam. *Hymenium* 25–36 μm tall; upper part dull greenish brown or olivaceous, K+ violet, with pigment confined to the gel-matrix; remaining (lower) part hyaline or dilute sordid greenish. *Asci* clavate, 25–35×7–10 μm. *Spores* ellipsoid, ovoid, or oblong-ovoid, not curved, sometimes with 1–3 guttules, simple but a few (very rarely many) sometimes 1-septate, (6·5–)7–9·5×2·0–3(–3·7) μm. *Paraphyses* scanty, sparingly branched 0·5–0·8 μm wide; apical parts often more richly branched, sometimes wider (to 1·5 μm), but without closely adhering pigment. *Hypothecium c.* 45–70 μm tall, hyaline, or dilute olivaceous (rarely dark olivaceous: 'f. *brasiliana*') and then K+ violet; hyphae interwoven but becoming vertically orientated towards the hymenium, *c.* 0·7–1 μm wide; ascogenous hyphae with swollen cells, *c.* 2–4 μm wide. *Excipulum* poorly developed but often evident as a dark brownish (K+ violet) zone bordering the reflexed edges of the hymenium; hyphae radiating, branched and anastomosing, very narrow, *c.* 0·5–0·8 μm wide.

Pycnidia usually present black, walls green-brown, K+ violet; of two types: (a) sometimes sessile, more usually borne single in the top of a black, unbranched stalk (pycnidiophore), 70–320 μm tall (including stalk) and 50–100 μm wide; stalk part composed of interwoven hyphae, *c.* 1–1·5 μm wide, embedded in a gel-matrix containing a dull brown or olivaceous, K+ violet pigment; *conidia* (*mesoconidia*) shortly cylindrical, sometimes faintly biguttulate, 3·5–5×1–1·5(–1·7) μm; (b) ± immersed in the substratum (lignum) or areolae, *c.* 40 μm diam; wall with green-brown, K+ violet pigment in upper part, but becoming ± hyaline below; conidia (microconidia) narrowly cylindrical, 3·8–6×0·6–0·8 μm. Pycnidia with stalks (a) are mostly confined to forms with an endoxylic thallus.

Chemistry: Sections of thallus (when superficial) K–, C+ red, PD–; sections of apothecia C+ violet (olivaceous pigment), but only rarely C+ red; t.l.c.: gyrophoric acid detected in varying amounts, sometimes absent.

Observations: Typical forms of *M. misella* with an endoxylic thallus, numerous apothecia, and stalked pycnidia are easy to recognize. However, when it has a well developed superficial thallus

Table 7 Diagnostic features for the separation of *Micarea denigrata* and *M. misella*.

	misella	*denigrata*
Apothecia size (mm)	0·1–0·3	0·1–0·5
Thallus type	Usually endoxylic; sometimes with areolae, 60–120 μm diam	usually with areolae, 60–200 μm diam; rarely endoxylic
Spore septation	0(–1)	(0–)1
Spore length (μm)	6·5–9·5	(7–)9–16(–18)
Paraphyses	sparse; 0·5–0·8 μm wide	numerous; 1–1·7 μm wide
Hymenium	C+ violet; very rarely also C+ orange-red	C+ violet; usually also C+ orange-red
Macroconidia (μm)	unknown	12–24×1; curved
Mesoconidia (μm)	3·5–5×1–1·5	2·8–4·5(–5)×1·2–1·8
Microconidia (μm)	3·8–5×0·6–0·8	(4·5–)5–7·5×0·7–0·8
Pycnidia (meso-)	sessile to stalked	immersed to emergent, never stalked
Chemistry (t.l.c.)	nil; but gyrophoric acid sometimes present in trace amounts, rarely in large amounts	gyrophoric acid usually present in large amounts; very rarely not detectable

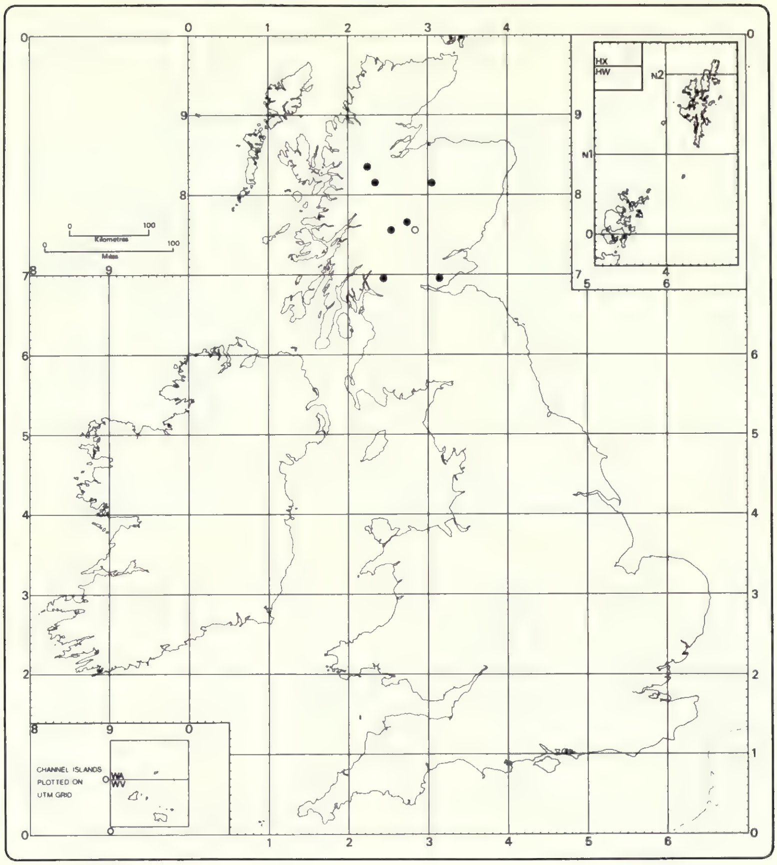
and no stalked pycnidia it can be difficult to separate from *M. denigrata*, especially if in the latter no conidial (or only the microconidial) state can be found. In such instances *M. misella* can usually be distinguished by its small apothecia, mainly simple, uncurved ascospores and sparse, thin paraphyses. The same criteria can separate forms of both species with an endoxylic thallus and lacking diagnostic macroconidial or mesoconidial states. A C+ orange-red reaction can usually be obtained in sections of the apothecia of *M. denigrata*, although the reaction is sometimes very weak or unobtainable in diminutive, lignicolous, epixylic forms; in *M. misella* I have obtained this reaction in only one or two extremely well-developed specimens. Table 7 outlines the main diagnostic features of these two species. Apart from *M. misella,* black, stalked pycnidia are also a characteristic feature of *M. botryoides*, *M. melaeniza*, and *M. nigella*; however, the pycnidial wall tissue in these species is brownish or greenish in KOH, and never violaceous as in *M. misella*.

For differences from *M. melanobola* and *M. prasina* see Table 6.

Habitat and distribution: M. misella is almost exclusively lignicolous (especially on conifer lignum). It has not been found on bark, but has been collected on *Picea* cones, old basidiomes of polypores (*Daedaleopsis confragosa* and *Gloeophyllum sepiarum*), and on moribund *Polytrichum* spp. by woodland tracks. Most British collections of *M. misella* have been made from the sides and undersides of fallen decorticated trunks of *Pinus*, and associated species included *Lecidea icmalea, Micarea prasina, Xylographa abietina, X. vitiligo, Cladonia* spp. (scattered squamules), and *Hypogymnia physodes*. Reports on exposed roots and stones (e.g. Watson, 1930: 53) refer to other species, especially *M. bauschiana*. In Britain *M. misella* appears to be rather rare and restricted to Scotland where it is mainly found in the native pine-woods. It has been reported (as '*Lecidea asserculorum*') from England and Wales, but all the pertinent material seen belongs to diminutive forms of *M. denigrata* and *M. prasina,* or quite different species such as *M. melaena* and *Cliostomum griffithii*.

M. misella is widely distributed in Europe, especially in areas with naturally occurring coniferous forests. It is found as far north as Lycksele Lappmark and Norbotten in Sweden, and an outlying southerly locality is on the Mediterranean island of Corsica where it was collected on the rotting lignum of *Eucalyptus*. From outside Europe I have seen material of *M. misella* from Canada (Ontario and Newfoundland), and from the highlands of Minas Geraes (at 1400 m) in Brazil.

Exsiccata: Arnold *Lich. Exs.* 626, 627 (BM ex K, M). Arnold *Lich. Mon.* 172, 241, 307 (BM ex K, M, MANCH). Britz. *Lich. Exs.* 208 (M). Claudel & Harm. *Lich. Gall.* 445 (BM). Crombie *Lich. Brit.* 174



Map 13 *Micarea misella* ● 1950 onwards ○ Before 1950

p.p. (BM). Elenkin *Lich. Ross.* 189 (UPS). *Krypt. Exs. Vindob.* 1532 (BM, BM ex K, M), 4214 (BM ex K, M). Malme *Lich. Suec.* 365 (S, WIS). Norrlin & Nyl. *Herb. Lich. Fenn.* 744 (H). *Reliq.* Suza. 42 (BM, GZU, WIS). Vainio *Lich. Bras.* 1420 (BM ex K, M), 1451 (BM). Zwackh *Lich. Exs.* 1085 (M).

27. **Micarea muhrii** Coppins, **sp. nov.**
(Fig. 23B)

Thallus effusus, endoxylicus et labem albidam efficiens, vel epixylicus aut epilithicus; thallus superficialis cum areolis convexis, albidus, *c.* 0·06–0.2 mm diam, interdum coalescentibus in crustam crassiusculam demum rimosam. *Algae* cellulis 4–7 μm diam. *Apothecia* adnata, convexa vel hemisphaerica autem haud globosa, griseo-atra, aut pallida vel rufo-brunneola vel fumosa ubi umbrose, 0·15–0·46 mm diam, immarginata sed vulgo zona marginali, complana, ± incolorata. *Hymenium* 40–45 μm altum, parte summa obscure olivacea vel griseo-viridi et K−, vel raro hyalina. Ascosporae ellipsoideae, ovoideo-ellipsoideae vel oblongo-ellipsoideae, simplices, 9–12×4–5 μm. *Paraphyses* aliquantum paucae, ramosae et interdum anastomosantes, 1–1·5 μm latae, apices versus vulgo incrasstae ad 3·5 μm latae et vulgo pigmentiferae. *Hypothecium* obscure rufofuscum, K−, HNO_3−. *Excipulum* hyalinum, paulum evolutum mox reflexum. *Pycnidia* pauca, immersa. *Conidia* cylindrica, 4–6×0·8–1 μm. *Thallus* et apothecia K−, C−, PD−; sine materia chemica.

Typus: Suecia, Wermelandia, par. Lungsund, Pungbäcken, alt. *c.* 170 m, in loco aperto ad truncum decorticatum supra rivum, 15 vii 1980, leg. *L.-E. Muhr* 2851 (E – holotypus). [t.l.c.: no substances.]

Thallus effuse, endoxylic and visible as a white stain, or epixylic, or rarely epilithic; superficial thallus formed of whitish, greenish-white or grey-white, convex areolae, *c.* 0·06–0·2 mm diam, which are especially well developed around the apothecia; areolae sometimes coalescing to form a thickish crust up to 0·2 mm thick, which may eventually become rimose. Areolae in section without a hyaline amorphous covering layer. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia numerous, occasionally coalescing, adnate, convex, soon becoming hemispherical, but never globose or tuberculate, grey-black, or pallid, reddish brown or brown-grey in shade forms, 0·15–0·46 mm diam; disc matt or slightly glossy; immarginate but the adnate rim is often seen as a ± colourless or watery grey zone, *c.* 20–40 μm wide. *Hymenium* 40–45 μm, ± hyaline with upper part dark olivaceous or grey-green, K−, HNO_3+ purple-red, or ± hyaline throughout in shade forms. *Asci* cylindrical-clavate, 38–40×10–12 μm. *Spores* simple, often biguttulate, ellipsoid, ovoid-ellipsoid or oblong-ellipsoid, 9–12×4–5 μm. *Paraphyses* rather scanty, branched (especially in their upper parts), sometimes anastomosing, 1–1·5 μm wide, often slightly incrassate at apices to 2 μm wide; or upper 9–15 μm of paraphyses thickened by dense greenish pigment and then to 3·5 μm wide. *Hypothecium c.* 70–120 μm tall, dark reddish brown, K−, HNO_3−; hyphae *c.* 1–2 μm wide embedded in the densely pigmented matrix, interwoven but becoming vertically orientated towards the hymenium; ascogenous hyphae with short, swollen cells to 5 μm wide. *Excipulum* sometimes evident in sections of young apothecia as a non-amyloid, hyaline zone, but soon reflexed and obscured in older apothecia; composed of radiating, branched and anastomosing hyphae 1–1·5(–2) μm wide.

Pycnidia rare, sunken within the areolae, *c.* 40–50 μm diam; upper part of wall around the ostiole olivaceous, lower part reddish brown, all parts K−. *Conidia* (*microconidia*) cylindrical, 4–6×0·8–1 μm.

Chemistry: Thallus K−, C−, PD−; apothecia sections C−; no substances detected by t.l.c.

Observations: Micarea muhrii is characterized by its convex-adnate, never tuberculate, usually dark grey apothecia, greenish upper hymenium, dark reddish brown hypothecium (without green or purple tinges, even in K), and simple spores. It recalls the mainly saxicolous *M. lutulata* in its pigmentation, but that species differs in having convex-subglobose, often tuberculate apothecia, smaller spores, and a larger celled phycobiont. The lignicolous *M. melaeniza* is another species with similar pigmentation, but has smaller, markedly convex to tuberculate apothecia, smaller spores, and sessile or stalked pycnidia.

Habitat and distribution: Often in abundance on lignum of decorticate logs that lie across streams and probably become inundated at times; collected once on a periodically inundated boulder in a stream. So far, known only from Värmland in Sweden, from where it has been found in at least four localities by Lars-Erik Muhr, in whose honour I have the pleasure of naming this species.

28. **Micarea myriocarpa** V. Wirth & Vězda ex Coppins, **sp. nov.**
(Figs 23C, 47C; Map 14)

Micarea myriocarpa V. Wirth & Vězda *in* Poelt & Vězda, *Bestimmungsschl. europ. Flechten, Erganzungsheft* I: 161 (1977); *nom. nudum* (Art. 32). – *Micarea myriocarpa* V. Wirth & Vězda *in* V. Wirth, *Flechtenfl.*: 341, 345 (1980); *nom. nudum* (Art. 32).

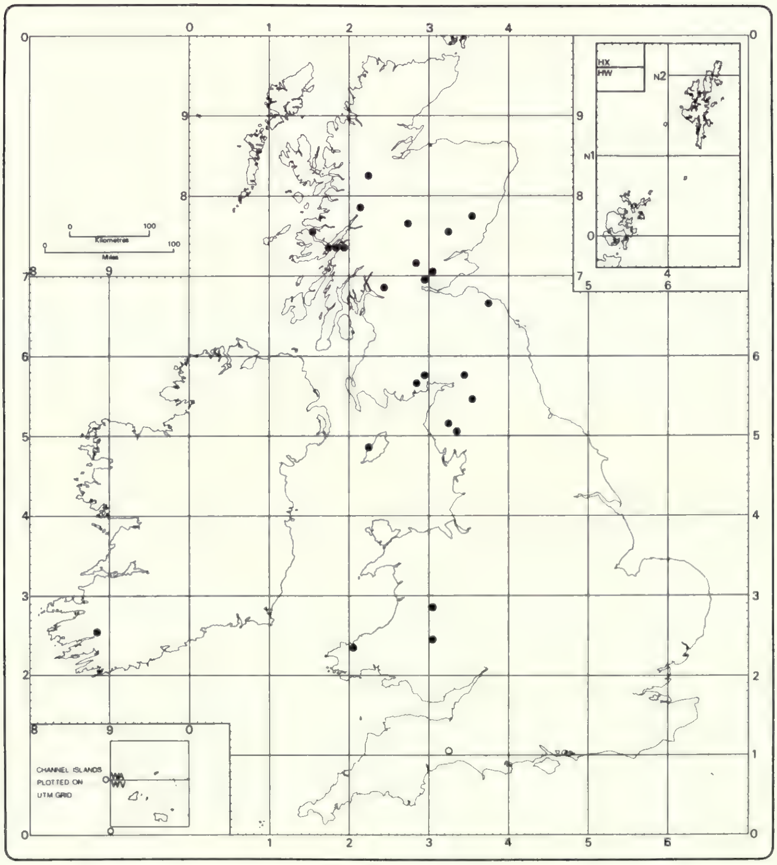
Thallus effusus, farinoso-granulosus, tenuissimus vel crassiusculus ad 0·3 mm crassus, pallide viridis vel viridulo-fulvus. *Algae* cellulis ± globisis, *c.* 4–7 μm diam, conglomeratis in granula goniocystiformes. *Apothecia* immarginata, primum convexo-hemisphaerica mox tuberculata, pallide vel obscure rufa, vel fusca, 0·1–0·25 mm diam. *Hymenium* 25–35 μm altum, ± hyalinum vel dilute rufo-brunneolum, cum vittis verticalibus obscure rufo-brunneolis, K−. *Ascosporae* oblongae vel oblongo-ovoideae, rectae vel ± curvatae, 5·5–8·5×1·5–2·5 μm. *Paraphyses* aliquantum paucae, dimorphae: *p.p.* hyalinae, laxae, simplices vel parce ramosae, interdum anastomosantes, graciles, 0·8–1·2 μm latae, apicibus interdum incrassatis ad 1·8 μm latis; *p.p.* pigmentiferae, fasciculatae, plerumque simplices, crassae, 2–3 μm latae. *Hypothecium* rufo-fuscum vel armeniaco-fuscum, K−, HNO_3−. *Excipulum* nullum. *Pycnidia* pauca et inconspicuosa, ±

sessilia, doliiformia, rufo-fusca, *c.* 25–30 μm diam. *Conidia* breviter cylindrica, 2·5–3·2×1–1·3 μm. *Thallus* et *apothecia* K−, C−, PD−; sine materia chemica.

Typus: Germania: 'Baden, Nordschwarzwald, Schurmsee bei Schönmünzach bei Schwarzenberg, alt. 790 m, Tannen am Seeausfluss', 25 v 1976, leg. *V. Wirth* (hb V. Wirth 6085 – holotypus!).

Thallus effuse, pale green or greenish buff, scurfy farinose-granular, thin or thickish up to 0·3 mm thick. *Phycobiont* ?micareoid, grouped into small goniocyst-like clusters *c.* 10–15 μm diam; cells ± globose 4–7 μm diam, or ellipsoid 5–7×3·5–5 μm.

Apothecia numerous, immarginate, at first convex-hemispherical, soon becoming ± globose, often becoming tuberculate, pale to dark reddish brown, rarely brown-black, 0·1–0·15 mm diam, or to 0·25 mm diam when tuberculate. *Hymenium c.* 25–35 μm tall, hyaline or dilute brownish, with dark brown, vertical streaks due to fasciculate pigmented paraphyses; K−, HNO_3−. *Asci* cylindrical-clavate, 21–25×5–7 μm. *Spores* oblong or oblong-ovoid, straight or slightly curved, simple or 1-septate, 5·5–8·5×1·5–2·5 μm. *Paraphyses* rather scanty, of two types: *p.p.* hyaline throughout, evenly distributed, simple or sparingly branched (especially above), sometimes anastomosing, thin, 0·8–1·2 μm wide, sometimes widening towards their apices to 1·8 μm; *p.p.* pigmented ± throughout, in small fasciculate clusters arising from the hypothecium, stout, 2–3 μm wide. *Hypothecium* 35–85 μm tall, reddish brown or dull orange-brown, K−, HNO_3−; hyphae coated with dense brownish pigment and *c.* 2–3 μm wide, interwoven but becoming vertically orientated towards the hymenium and sometimes continuing into it as pigmented, fasciculate paraphyses; ascogenous hyphae similarly pigmented but with short swollen cells, to 4 μm wide. *Excipulum* not evident, even in sections of young apothecia.



Map 14 *Micarea myriocarpa* ● 1950 onwards ○ Before 1950

Pycnidia occasionally present but very inconspicuous, ± sessile, doliiform reddish brown, *c.* 25–35 μm tall and 25–30 μm diam; wall reddish brown or dull orange-brown, K−, HNO_3−. *Conidiogenous cells* ± cylindrical to ampulliform, 4–5×1–1·2 μm but base sometimes swollen to 2 μm wide. *Conidia* (*mesoconidia*) short cylindrical, sometimes faintly biguttulate, 2·5–3·2×1–1·3 μm.

Chemistry: Thallus K−, C−, PD−; apothecia sections C−; no substances detected by t.l.c.

Observations: Micarea myriocarpa is characterized by its numerous, small, ± globose to tuberculate, reddish brown apothecia, darkish (but never blackish, even in thick sections) hypothecium, and small, narrow, 0–1-septate spores. The apothecial tissues completely lack any greenish pigmentation, unlike in *M. tuberculata* and *Psilolechia clavulifera*, species of similar habitats with which *M. myriocarpa* has been confused. *M. botryoides* is another common associate of *M. myriocarpa*, but can be distinguished by its black apothecia, darker hypothecium, larger spores, and numerous stalked, black pycnidia.

Habitat and distribution: M. myriocarpa is faithful to the *Micareetum sylvicolae* and is found especially on exposed roots in dry underhangs under trees on steep slopes in valley woodlands. In the same situations it has been collected also on loose stones and mats of dry bryophytes. An additional habitat for *M. myriocarpa* is the dry undersides of stumps (especially conifers), situations which are microclimatically identical to rocky underhangs. In Britain, *M. myriocarpa* is widely distributed, but little collected, in western and northern districts. On the Continent the species is little known, but I have seen material from western Norway as far north as Trondheim, and Värmland in Sweden; and Wirth (*loc. cit.*) records it from the northern Schwarzwald in Germany (the type locality).

29. **Micarea nigella** Coppins, **sp. nov.**
(Figs 24A, 47B; Map 15)

Thallus effusus, immersus vel tenuissimus, albidus vel viridi-griseus. *Algae* cellulis 4–7 μm diam. *Apothecia* primum subglobosa mox tuberculata, immarginata, atra, 0·1–0·3 mm diam. *Hymenium* 25–30 μm altum, ± incoloratum, autem parte summa (epithecio) purpureo-fusca K+ olivacea. *Ascosporae* ellipsoideae, ovoideae vel oblongo-ovoideae, simplices 6·5–11×2·5–4 μm. *Paraphyses* aliquantum paucae, dimorphae: *p.p.* hyalinae, laxae, ramosae, gracillimae, 0·7–1 μm latae, apicibus vulgo leviter incrassatis ad 2 μm latis; *p.p.* pigmentiferae, fasciculatae, plerumque simplices, crassae, 2–2·5 μm latae. *Hypothecium* obscure purpureo-fuscum, K+ obscure olivaceum. *Excipulum* paulum evolutum mox reflexum. *Pycnidia* numerosa, atra, sessilia vel stipitata, interdum ramosa, *c.* 40–300 μm alta et 40–80 μm lata, parietibus purpureo-fuscis, K+ obscure olivaceis. *Conidia* ellipsoidea ad breviter cylindrica, 3·4–4·3×1·2–1·6 μm. *Thallus* et *apothecia* K−, C−, PD−.

Typus: Dania, Jyllandia, *c.* 16 km septentriones e Hobro, Rold Skov, Torstedlund Skov, ad truncum decorticatum vetustum coniferarum in sylva mixta, 8 viii 1979, *B. J. Coppins* 4429 (E – holotypus).

Thallus effuse, endoxylic, or ± epixylic as a thin whitish to pale green-grey crust, but not forming discrete granules or areolae. *Phycobiont* micareoid, cells 4–7 μm diam.

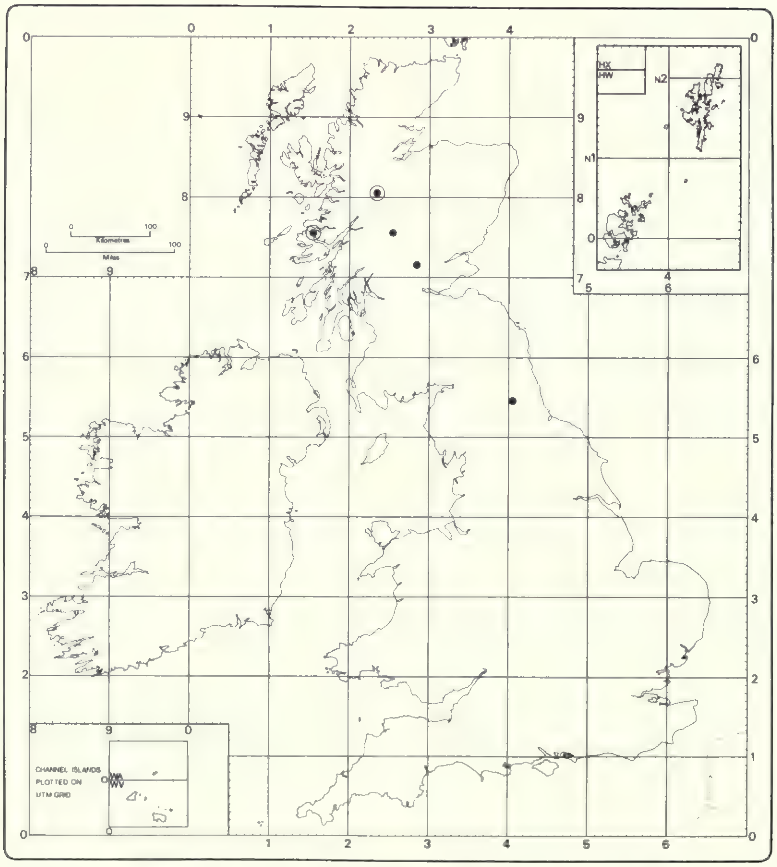
Apothecia few to numerous, immarginate, subglobose at first, often becoming tuberculate, black, matt, 0·1–0·2 μm diam, or to 0·3 mm diam when tuberculate. *Hymenium* 25–30 μm tall, hyaline or tinged dull purplish brown in places, often with darker, purplish brown vertical streaks; upper part (2–15 μm) irregularly pigmented purplish brown; K+ dull green, HNO_3+ red. *Asci* clavate, 22–27×10–11 μm. *Spores* ellipsoid, ovoid or oblong-ovoid, simple, 6·5–12×2·5–4 μm. *Paraphyses* scanty, of two types: *p.p.* evenly distributed, branched, hyaline, thin, 0·7–1 μm wide, with apices sometimes widening to 2 μm but not becoming pigmented although embedded in pigmented gel-matrix; *p.p.* scattered or in small fascicles, mostly simple, stout, 2–3 μm wide, coated ± throughout by dark pigment. *Hypothecium* 70–100(–160) μm tall, mottled, dark purplish brown, K+ dark dull green, HNO_3+ purple-red; hyphae coated with dense pigment and *c.* 1·5–3 μm wide, interwoven but becoming vertically orientated towards the hymenium and sometimes continuing into it as stout, pigmented paraphyses; ascogenous hyphae similarly pigmented but with short, swollen cells, to 4 μm wide. *Excipulum* indistinct;

sometimes evident in young apothecia as a dark (concolorous with hypothecium) narrow zone forming an edge to the reflexed part of the hymenium; hyphae radiating, branched and anastomosing, *c.* 0·8–1·5 μm wide.

Pycnidia numerous, black, sessile or more usually stalked, 60–300 μm tall (including stalk) and 40–80 μm diam; stalks (pycnidiophores) simple or sometimes branched bearing up to 4 pycnidia; stalk and pycnidial wall tissues dark purplish brown, K+ dark green, HNO_3+ purple-red. *Conidiogenous cells* 4·4–7·6 μm tall, with a cylindrical neck 1·9–3·7 μm tall and 0·8–1·4 μm wide, and with a swollen base 2·4–3(–3·7) μm wide, the wall of which is often pigmented; percurrent proliferations not seen. *Conidia* (*mesoconidia*) ellipsoid or short cylindrical, sometimes faintly biguttulate, 3·4–4·3×1·2–1·6 μm.

Chemistry: Thallus K−, C−, PD−; apothecia sections C−; no substances detected by t.l.c.

Observations: Micarea nigella belongs to the group of lignicolous species (including *M. contexta, M. eximia, M. melaeniza, M. misella, M. olivacea*, and *M. rhabdogena*) with an endoxylic or indistinct thallus and small, ± globose to tuberculate, black apothecia. It is characterized by the purple-brown, K+ green pigment in the hymenium, hypothecium and pycnidial tissues, simple spores and stalked pycnidia. It is most likely to be confused in the field with other species with stalked, black pycnidia, namely *M. melaeniza* and *M. misella. M. melaeniza* differs in having a bright green hymenium, a red-brown hypothecium that does not turn green in K, a different pycnidial pigmentation and shorter mesoconidia. *M. misella* has a K+ violet hymenium, a ± hyaline hypothecium and an olivaceous, K+ violet pigment in the pycnidial wall tissues. Apart from their lack of stalked pycnidia, *M. contexta, M. eximia,* and *M.*



Map 15 *Micarea nigella* ● + *Micarea olivacea* ◉

olivacea can be distinguished from *M. nigella* by their 1-septate spores. *M. rhabdogena* has a brown (K+ dissolving) pigment in the upper hymenium, and smaller spores. *M. nigella* could be confused with diminutive lignicolous forms of *M. melaena*, but that species usually has a bright green hymenium, larger and 1–3-septate spores, and never has stalked pycnidia.

Habitat and distribution: M. nigella occurs on rather soft lignum of stumps of conifers and birch, in deeply shaded situations. Primarily, it appears to be an inhabitant of conifer woodlands, and has been found both in native pine forest (Black Wood of Rannoch) and mature conifer plantations. It is known from only three localities: north Jylland in Denmark, the southern central highlands of Scotland and north-east England; and, although undoubtedly a rather rare species, it has surely been much overlooked, at least in north-west Europe.

30. Micarea nitschkeana (Lahm ex Rabenh.) Harm.
(Fig. 24B; Map 16)

in *Bull. Soc. Sci. Nancy* II, **33**: 64 (1899). – *Bilimbia nitschkeana* Lahm ex Rabenh., *Lich. Europ. Exs.* 583 (1861). – *Micarea denigrata* var. *nitschkeana* (Lahm ex Rabenh.) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 79, 90 (1892). – *Bacidia nitschkeana* (Lahm ex Rabenh.) Zahlbr. in *Annln naturh. Mus. Wien* **22**: 342 (1905). Type: Germany, Nordrhein-Westfalen, between Münster and Nobriskrug, on *Pinus* in wood, *T. R. J. Nitschke,* Rabenh. *Lich. Eur. Exs.* 583 (M – lectotype!; isolectotypes: BM!, BM ex K!, M!).

Lecidea spododes Nyl. in *Flora, Jena* **52**: 410 (1869). – *Bacidia spododes* (Nyl.) Zahlbr., *Cat. lich. univ.* **4**: 151 (1926). Type: England, Hampshire, Lyndhurst, New Forest, old pales, *J. M. Crombie* (H-NYL 18819 – lectotype!; isolectotypes: BM!, H-NYL 18820!).

Bacidia nitschkeana f. *microcarpa* Erichsen in *Verh. bot. Ver. Prov. Brandenb.* **71**: 97 (1929). Type: West Germany, Schleswig-Holstein, Eckernförde, near Levensau, Felmerholz, on *Picea* twigs, 9 xi 1924, *C. F. E. Erichsen* (HBG – holotype!).

?Bilimbia spododes f. *fusca* B. de Lesd., *Rech. Lich. Dunkerque*: 200 (1910). Type: France, Nord, Dunkerque, Malo-Terminus, on dead branch of *Hippophae, B. de Lesdain* (not seen).

?Bilimbia spododes f. *livida* B. de Lesd., *Rech. Lich. Dunkerque,* Suppl. I: 120 (1914). Type: France, Nord, Dunkerque, Zuydcoote, on dead branch of *Hippophae, B. de Lesdain* (not seen).

?Bilimbia spododes var. *nigra* B. de Lesd., *Rech. Lich. Dunkerque,* Suppl. I: 120 (1914). Type: France, Nord, Dunkerque, Malo-Terminus, dunes, on dried rhizome of *Ammophila arenaria, B. de Lesdain* (not seen).

Thallus effuse, usually forming small patches but sometimes wide-spreading, sometimes partly endoxylic but usually developed on the surface of the substratum as crowded, often contiguous, convex to subglobose areolae. Areolae especially well developed around the apothecia, dull greenish white to green-grey, surface matt, *c.* 40–200 μm diam; in section, without a well defined cortex and not surrounded by an amorphous covering layer, outermost hyphae sometimes surrounded by dilute olivaceous, K+ violet pigment. Thallus sometimes blackish and scurfy due to disruption by invading dematiaceous fungi and non-lichenized algae. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia scattered or, more usually, numerous and crowded, frequently contiguous or confluent, adnate, plane to convex-hemispherical, sometimes becoming tuberculate, immarginate or occasionally (especially when young) with an indistinct margin that is flush with the level of the disc, grey-black to black, or rarely whitish to pale grey-brown (shade forms), sometimes paler at the margin, matt. *c.* 0·1–0·3 mm diam, or to 0·4 mm diam when tuberculate. *Hymenium* 30–40 μm tall, upper part dilute olivaceous to olivaceous, K+ violet, HNO_3+ red, C+ violet, also C+ orange-red throughout due to gyrophoric acid; olivaceous pigment mostly confined to the gel-matrix, only rarely (in old, dark apothecia) closely bound to the walls of the paraphyses. *Asci* clavate 25–40×9·5–11 μm. *Spores* fusiform, mostly curved, (1–)3(–4)-septate, 10–17(–19)×2·5–3(–3·5) μm. *Paraphyses* numerous, branched and anastomosing 1–1·5(–1·7) μm; apices not or only slightly incrassate, and mostly without closely adhering pigment. *Hypothecium* 30–50 μm tall, hyaline; hyphae interwoven, *c.* 1–1·5 μm wide; ascogenous hyphae with swollen cells *c.* 2–5 μm wide. *Excipulum* distinct in sections of young, ± plane apothecia, but reflexed and obscured in older, more convex apothecia; hyaline or dilute olivaceous (K+ violet) at outer edge; hyphae radiating, branched and anastomosing, *c.* 1–1·5 μm wide.

Pycnidia indistinct but usually present, immersed in areolae; walls hyaline throughout, or olivaceous (K+ violet) around the ostiole; of three types: (a) *c.* 60–80 μm diam, ostiole sometimes widely gaping; *Conidia* (*macroconidia*) curved or hamate, 1–3-septate, 12–26×*c.* 1 μm; (b) *c.* 50–100 μm diam, ostiole often gaping and conidia extruded as a white blob; *conidia* (*mesoconidia*) short-cylindrical or obovate-oblong, apices rounded but often distinctly truncate at proximal end, sometimes biguttulate, (3–)3·5–5(5·7)×1–1·5 μm; (c) *c.* 40–50 μm diam, ostiole never gaping; conidia (microconidia) narrowly fusiform or bacilliform, (4·7–)5·5–7·5×0·7–0·8 μm.

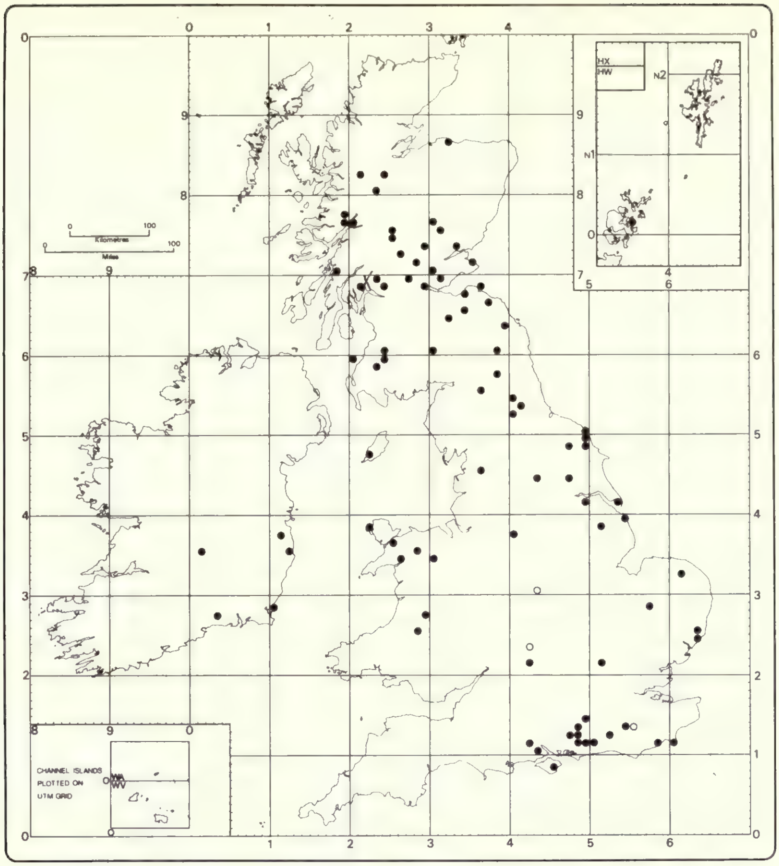
Chemistry: Thallus K−, PD−; sections of thallus and apothecia C+ orange-red (also, parts with olivaceous pigment, C+ violet); t.l.c.: gyrophoric acid. If thallus is heavily parasitized and scurfy the C+ orange-red reaction may be difficult to obtain and gyrophoric acid may not be detectable by t.l.c.

Observations: M. nitschkeana is closely related, and similar in most respects, to *M. denigrata* (*q.v.*) with mainly 1-septate spores, and *M. globulosella* (*q.v.*) with ± acicular or rod-shaped 0–3(–6)-septate spores. Like *M. denigrata, M. nitschkeana* has three pycnidial anamorphs; usually only one or two of these states are found on any given thallus, but all three states (plus apothecia) have been noted on a single specimen from Scotland (*Coppins* 3369). In the field *M. nitschkeana* can be confused with species such as *M. cinerea, M. lignaria*, and *M. peliocarpa*, but these species usually have larger apothecia and areolae, and are quite different when examined microscopically.

Habitat and distribution: M. nitschkeana is widely distributed in the British Isles at low altitudes (below 300 m), and is most frequently found on twigs or small branches of various deciduous and coniferous trees, e.g. *Acer, Aesculus, Alnus, Betula, Fraxinus, Prunus padus, Quercus, Salix, Sambucus, Larix,* and *Picea*; or on the old or dead stems of smaller shrubby plants, especially *Calluna* and *Ulex*, but also *Erica cinerea, Myrica, Rosa, Sarothamnus, Viburnum,* and *Juniperus*. It has been found to be abundant on old stems and litter of *Calluna* in some lowland heaths in eastern England (Coppins & Shimwell, 1971), Scotland and Denmark, where it is commonly associated with *Lecanora conizaeoides* and *Scoliciosporum chlorococum*; such communities are referable to the *Bacidietum chlorococcae*. Other associated species on twigs and small branches include *Lecanora pulicaris, L. symmicta* agg., *L. icmalea, Mycoblastus sterilis, Fuscidea lightfootii* (western districts), *Micarea prasina, Graphis elegans, Stenocybe pullatula* (on *Alnus*) and small thalli of *Hypogymnia physodes, H. tubulosa, Parmelia subaurifera, P. sulcata, Platismatia glauca, Evernia prunastri,* and *Ramalina fairinacea*. It has occasionally been met with on lignum of fallen conifers (*Larix* and *Pinus*) or fence posts, habitats more characteristic of *M. denigrata*. Associated species on lignum include *Lecanora confusa, L. symmicta* agg., *Lecidea granulosa* agg., *L. icmalea, Mycoblastus sterilis, Hypogymnia physodes, Parmelia saxatilis,* and *Platismatia glauca*. Occurrences on rock are rare, but a few collections have been made on sandstone or flint stones in heathland, with *Lecidea granulosa* agg., *L. icmalea,* and *Micarea melaena* as associates. It has also been found together with *Scoliciosporum umbrinum* on a plastic carton in a heathland in the Isle of Wight (Brightman & Seaward, 1977).

M. nitschkeana is widely distributed through much of northern Europe. In Scandinavia it has a southern distribution and I have not seen material of it from north of latitude 62°N. It usually occurs in lowland situations, but it attains higher altitudes in the Alps (920 m) and the Nízke Tatry of Czechoslovakia (1250 m). Additional phorophytes from extra-British material include *Hippophae* (France: dunes near Calais), *Vaccinium uliginosum* (Germany: Schleswig-Holstein), and *Pinus mugo* subsp. *pumilio* (heathlands of southern Germany). From outside Europe I have seen only one specimen: USA, northern California (near San Francisco), where it occurred on fence posts.

Exsiccata: Arnold *Lich. Exs.* 217 (BM ex K, M), 503 A, B (H-NYL, M); 503 C (BM ex K, H-NYL, M), 503 D (H-NYL, M). Arnold *Lich. Mon.* 48 (BM ex K, M); 270 (BM ex K). Britz. *Lich. Exs.* 829 (M).



Map 16 *Micarea nitschkeana* ● 1950 onwards ○ Before 1950

Claudel & Harm. *Lich. Gall.* 89 (L, O). Harm. *Lich. Loth.* 853 (M). Hepp *Flecht. Eur.* 20 (BM, E, L, M), 21 *p.p.* (E). *Krypt. Exs. Vindob.* 1232 (M). Lojka *Lich. Univ.* 137 (BM ex K, M). Magnusson *Lich. Sel. Scand.* 340 (M). Malbr. *Lich. Norm.* 287 (M). Malme *Lich. Suec.* 25 (M, S). Rabenh. *Lich. Eur.* 582, 583 (BM, BM ex K, M). Räsänen *Lich. Fenn.* 642 (M). Zahlbr. *Lich. Rar.* 110 (BM). Zwackh *Lich. Exs.* 470 ['bei Münster in Westfalen'] (H-NYL 18825), 470 bis ['Bei Delbrueck in Kreise Paderborn.'] (H-NYL 18822, M), 534 (H-NYL, M), 587 (H-NYL, M).

31. **Micarea olivacea** Coppins, **sp. nov.**
(Figs 24C, 47A; Map 15)

Thallus effusus, endoxylicus vel epixylicus aut epilithicus, tenuissimus, inaequalis, interdum leviter areolatus, albidus vel viridio-griseus. *Algae* cellulis 4–7 μm diam. *Apothecia* immarginata, primum convexa vel subglobosa mox tuberculata, atra, 0·1–0·3 mm diam, aut ad 0·4 mm diam ubi tuberculata. *Hymenium* 30–35 μm altum, dilute sordide olivaceum cum vittis verticalibus atro-olivaceis, K+ clare olivaceo-virescens. *Ascosporae* oblongae vel ovoideo-oblongae, rectae, (0–)1-septatae, (7–)9–12·3×2·5–3·5 μm. *Paraphyses* numerosae, dimorphae: *p.p.* hyalinae, laxae, ramosae et anastomosantes, graciles, *c.* 1–1·2 μm latae, apicibus interdum leviter incrassatis ad 2 μm latis; *p.p.* pigmentiferae, fasciculatae, plerumque simplices, crassae, 2–3 μm latae. *Hypothecium* sordide atro-olivaceum vel olivaceo-fuscum, K+ virescens. *Excipulum* paulum evolutum mox reflexum. *Pycnidia* numerosa sed inconspicua, ± immersa, 25–50 μm diam., parietibus sordide olivaceis vel olivaceo-fuscis, K+ clare olivaceis. *Conidia* breviter cylindrica, 3–4·2×1–1·3 μm. *Thallus* et *apothecia* K−, C−, PD−.

Typus: Caledonia, Mull, Aros, Druimfin, in ligno duro, 15 v 1968, *P. W. James* (BM – holotypus).

Thallus effuse, endoxylic to epixylic, or epilithic, forming a thin, whitish grey or greenish grey, uneven, sometimes weakly areolate crust; often appearing scurfy due to invasion by foreign fungi and algae. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia numerous, immarginate, convex to subglobose, often tuberculate, black, matt or slightly glossy, surface minutely roughened, 0·1–0·25 mm diam, or to 0·4 mm diam when tuberculate. *Hymenium* 30–35 μm tall, without a distinct upper part (epithecium), dilute sordid olivaceous with dark olivaceous vertical streaks, K+ green intensifying, HNO_3+ red. *Asci* clavate, 35–33×9·5–11 μm. *Spores* oblong or ovoid-oblong, straight, (0−)1-septate, (7−) 9–12·3×2·5–3·5 μm. *Paraphyses* numerous, of two types: *p.p.* hyaline throughout, evenly distributed, branched and often anastomosing, rather thin, 1–1·2 μm wide, apices sometimes widening to 2 μm and sometimes with colourless, oily, refractive contents; *p.p.* broad, 2–3 μm wide, mostly simple, grouped in small fascicles and often embedded in dense pigment. *Hypothecium* 40–70 μm tall, dark sordid olivaceous or olive-brown, K+ green intensifying, HNO_3+ red; hyphae embedded in greenish gel-matrix but walls not deeply pigmented, *c.* 1·5–2 μm wide, interwoven but becoming vertically orientated towards the hymenium and sometimes continuing in to it as fasciculate paraphyses; ascogenous hyphae with short swollen cells, to 5 μm wide. *Excipulum* indistinct and soon reflexed, sometimes evident in sections of young apothecia as a hyaline or dilute sordid olivaceous, non-amyloid zone *c.* 20 μm wide; composed of radiating, much branched and anastomosing hyphae 0·8–1·5 μm wide.

Pycnidia numerous but inconspicuous, ± immersed, 25–50 μm diam; walls sordid olivaceous or olive-brown, K+ green intensifying, HNO_3+ red. *Conidiogenous cells* elongate-ampulliform to subcylindric, 4–5·5×1·5–3 μm. *Conidia* (*mesoconidia*) short cylindrical, sometimes faintly biguttulate, 3–4·2×1–1·3 μm.

Chemistry: Thallus K−, C−, PD−; apothecia sections C−; no substances detected by t.l.c.

Observations: Micarea olivacea differs from *M. eximia* in its less brightly coloured hymenium pigmentation that is not concentrated in the upper part, more numerous and broader paraphyses, shorter and slightly broader spores with rounded apices, and shorter mesoconidia. From *M. nigella* it can be distinguished by the complete absence of purple pigmentation in water mounts, more numerous and broader paraphyses, more elongate and 1-septate spores, and ± immersed (never stalked) pycnidia. *M. olivacea* is easily confused with epruinose forms of the common lignicole *Lecidea turgidula* Fr., but that species has a dark green or olive-brown excipulum of conglutinated hyphae that do not separate in K, a paler hypothecium, and a thick walled, large celled phycobiont with cells 12–16 μm diam. In addition, the conidia of *L. turgidula* are smaller, *c.* 3–3·5×1·5–1·8 μm. When on rock *M. olivacea* can be confused with *M. tuberculata*, but the latter has a more brightly coloured hymenium and hypothecium, somewhat smaller spores, narrower asci, and a non-micareoid phycobiont with cells *c.* 5–10 μm when globose or up to 15×7 μm when ellipsoid. *M. tuberculata* has similar pycnidia and conidia, but its conidiogenous cells are more slender and about twice as long as those of *M. olivacea*.

Habitat and distribution: M. olivacea is an apparently rare, but probably overlooked, species, being known from just two localities, both in Scotland. At the type locality it occurred on the hard lignum of a stump by a conifer plantation; the collection contains no associate species. At the other locality it occurred with *Rhizocarpon hochstetteri* and *Baeomyces rufus* on shaded rock in a mature conifer plantation. Little more can be said of its ecology until it becomes better known, but I am inclined to believe that it is essentially a lignicolous species with a preference for hard lignum. If this is true then care should be taken not to overlook it in the field for forms of the common *M. denigrata* with a reduced thallus.

32. **Micarea osloensis** (Th. Fr.) Hedl.
(Fig. 28B)

in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 83, 97 (1892). – *Lecidea osloensis* Th. Fr., *Lich. Scand.* **2**: 524 (1874). Type: Norway, Oslo, summit of Ryenbjerget, on decaying plant debris, *N. G. Moe* (UPS – holotype! [t.l.c.: no substances]).

Thallus effuse, indistinct, apparently of whitish grey, ± convex areolae, *c.* 50–70 μm diam, in the single specimen seen the thallus is obscured by a bleached non-lichenized alga, giving it a pale grey 'filmy' appearance. *Phycobiont* probably micareoid, cells 4·5–6·5 μm diam.

Apothecia numerous, ± evenly scattered, immarginate, convex to subglobose, black or brown-black, 0·1–0·26 mm diam. *Hymenium c.* 30 μm tall; upper part (epithecium) red-brown, K–, HNO_3– or red tinge intensifying; remaining (lower) part dilute reddish brown with darker, red-brown, vertical streaks. *Asci* clavate, 26–30×11–13 μm. *Spores* ellipsoid or ovoid-ellipsoid, simple, 6–9·5×3–4 μm. *Paraphyses* rather numerous, simple below, but mostly branched towards their apices, hyaline and 1·5–1·8 μm wide, but occasionally surrounded throughout their length by red-brown pigment and then 1·7–2 μm wide; apices sometimes swollen to 3 μm wide, surrounded by an amorphous, red-brown, pigmented matrix that does not disperse in K. *Hypothecium c.* 70–85 μm tall, dark reddish brown, K–, HNO_3– or red tinge intensifying. *Excipulum* not evident, even in sections of young apothecia.

Pycnidia not seen.

Chemistry: Thallus K–, C–, PD–; sections of thallus and apothecia C–; no substances detected by t.l.c.

Observations: Micarea osloensis is characterized by its small, blackish apothecia with internal reddish brown pigment that does not disperse in K, simple, ellipsoid spores, and terricolous habitat. In the field it is most likely to be overlooked for *Lecidea uliginosa*, but that species has a well developed, pseudoparenchymatous excipulum, paraphyses with a brown apical cap, larger spores, and 'Trapelioid' asci which do not have a deeply amyloid tholus.

Habitat and distribution: Knowledge of *M. osloensis* is still restricted to its type gathering from Norway. The appearance of this material suggests that it occurred in a woodland clearing on the site of an old bonfire (small amounts of ash are present), probably in a slight depression. The specimen is accompanied by the sterile thallus of *Lecidea icmalea* and a few plants of the moss *Ceratodon purpureus*. Dr H. Krog informs me that the hill Ryenberget is now well within the city limits of Oslo, and is now much affected by the results of urbanization, although not completely destroyed. It has an altitude of about 150–200 m, and was almost certainly covered in pine forest before it was engulfed by the city.

33. **Micarea peliocarpa** (Anzi) Coppins & R. Sant.
(Figs 3A–C, 25, 48, 53–54; Map 17)

in Coppins & P. James in *Lichenologist* **11**: 155 (1979). – *Bilimbia peliocarpa* Anzi in *Atti Soc. ital. Sci. nat.* **9**: 250 (1866). – *Bacidia peliocarpa* (Anzi) Lettau in *Hedwigia* **52**: 133 (1912). – *Micarea violacea* f. *peliocarpa* (Anzi) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 81, 92 (1892); *nom. superfl.* (Art. 63). Type: Italy, Piemonte, Novara, 'Sopra i muschi nei monti del Lago Maggiore (Locarno), scoperta dal padre capuccino Agostino Daldini' (? TO, not seen: request for loan not acknowledged); an unlocalized specimen labelled 'Bilimbia peliocarpa Anzi Neosymb. no. 44' [reference to original protologue] in Anzi's handwriting occurs in UPS(!) and is possibly an isotype.

Biatora lignaria β. [var.] *conglomerata* Hepp, *Flecht. Eur.*, fasc. 5, no. 284 (1857). – *Micarea violacea* f. *conglomerata* (Hepp) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 81, 92 (1892). Type: Switzerland, 'bei Rifferschweil', on *Pinus* bark, *Hegetschweiler,* Hepp *Flecht. Eur.* 284 (E – lectotype!; M – isolectotype!).

Biatora lignaria var. *saxigena* Hepp, *Flecht. Eur.* fasc. 9, no. 510 (1860). Type: Germany, Hessen, 'auf Sandsteinfelsen bei Marburg', *W. Uloth,* Hepp *Flecht. Eur.* 510 (E – lectotype!; M – isolectotype!). See note (i) below.

Bilimbia milliaria var. *lignaria* *[f.] *livida* Körber, *Parerga Lich.*: 171 (1860). Type: same as *Biatora lignaria* var. *conglomerata* Hepp.

Lecidea sphaeroides var. *leucococca* Nyl. *in* Stizenb. in *Nova Acta Leop. - Carol.* **34** (2): 18, t. 1, f. D, 47–51 (1867). Type: Finland, Tavastia australis, Evois ['Evo'], on lignum, 1865, *J. P. Norrlin* (H-NYL 18377–lectotype!; H – isolectotype!).

Bilimbia violacea Arnold in *Flora, Jena* **53**: 473 (1870). – *Lecidea violacea* P. Crouan & H. Crouan ex Nyl. in *Flora, Jena* **45**: 464 (1862), non Massal. (1852). – *Micarea violacea* (Arnold) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 80, 91 (1892). Type: France, Finistère, Brest, on schistose rock, *Crouan* (H-NYL 18716 – isotype!). [*Note*: listed as '*Bacidia violacea* (Crouan ex Nyl.) Arnold' by James (1965a); this should not be confused with *Bacidia violacea* (Arnold) Arnold, *Flora, Jena* **67**: 581 (1884), which is a *Bacidia* s. str.]

Bilimbia trisepta Hellb., *Nerikes Lafflora*: 77 (1871). – *Biatora trisepta* Naeg. ex Müll. Arg. in *Mem. Soc. Phys. Hist. nat. Genève* **16**: 403 (1862); as 'Naeg. mss. ex Dr Hepp', *nom. inval.* (Arts 32, 34). – *Lecidea sabuletorum* f. *trisepta* Stizenb. in *Nova Acta Acad. Leop.-Carol.* **34** (2): 47, t. 3, f. A, 35–62 (1867); *nom. superfl.* (Art. 63). – *Bilimbia hypnophila* b. [var.] *trisepta* Bausch in *Ver. naturw. Ver. Karlsruhe* **4**: 127 (1869); *nom. superfl.* (Art. 63). – *Bilimbia sabuletorum* d. [var.] *trisepta* Rabenh., *Krypt.-Fl. Sachsen* **2**: 187 (1870); *nom. superfl.* (Art. 63). – *Bacidia trisepta* (Hellb.) Zahlbr. in Engler & Prantl, *Nat. Pflanzenfam.* **1** (1*): 135 (1905). – *Micarea trisepta* (Hellb.) Wetmore in *Pub. Mus. Mich. St. Univ.* Biol. **3**: 284 (1968). Type: Germany, Hessen, 'auf Sandsteinfelsen bei Marburg', *W. Uloth,* Hepp *Flecht. Eur.* 510 (E – neotype!; M – isoneotype!). See note (ii) below.

Lecidea hemipolioides Nyl. in *Flora, Jena* **56**: 294 (1873). – *Bilimbia hemipolioides* (Nyl.) A. L. Sm., *Monogr. Br. Lich.* **2**: 141 (1911). – *Bacidia hemipolioides* (Nyl.) Zahlbr., *Cat. lich. univ.* **4**: 114 (1926). – *Micarea violacea* f. *hemipolioides* (Nyl.) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 80, 91 (1892). Type: Channel Islands, Jersey, Rozel meadow, on rocks, 1873, *C. Larbalestier* (H-NYL 18713 – lectotype!; isolectotypes: H-NYL p.m. 4613!, BM!).

Bilimbia naegelii f. *lapiseda* Th. Fr., *Lich. Scand.* **2**: 379 (1874). Type: Sweden, Stockholm, Lyran, on rock, 1870, *S. Almquist* (UPS – lectotype!).

Bilimbia milliaria f. *livescens* Th. Fr., *Lich. Scand.* **2**: 383 (1874). Type: Sweden, Närke, Gotlunda, 'på stenmuren mellan Stäbacken och Hogby', on mosses, 1863, *Blomberg* (UPS – lectotype!).

Lecidea albidolivens Nyl. in *Flora, Jena* **57**: 10 (1874). – *Bilimbia albidolivens* (Nyl.) Blomb. & Forss., *Enum. Pl. Scand.*: 82 (1880). Type: Finland, Tavastia australis, Padasjoki, Nyystölä, on lignum, 1872, *E. A. Lang [Vainio]* (H-NYL 18775 – lectotype!; H – isolectotype!).

Lecidea fraterculans Nyl. in *Flora, Jena* **58**: 11 (1875). Type: Finland, Tavastia australis, Padasjoki, Nysstölä, on rock, 1872, *E. A. Lang [Vainio]* (H-NYL 18704a – lectotype!; H-NYL 18704 – isolectotype!).

Lecidea triseptatula Nyl. in *Flora, Jena,* **58**: 361 (1875). Type: Finland, Tavastia australis, Hollola, on lignum, 1874, *E. A. Lang [Vainio]* (H-NYL 18709 – lectotype!; isolectotypes: H-NYL 18710!, H!).

Bilimbia albicans Arnold in *Flora, Jena* **65**: 140 (1882). Type: Germany, Bayern, Oberbayern, near Bad Tölz, W side of the Blombergs, on sandstone in wood, 5 ix 1880, *Arnold*, Lich. exs. 837 (BM – lectotype!).

Micarea violacea f. *cupreola* Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 80, 91 (1892). Type: Sweden, Hälsingland, Järvsö, on rock, viii 1891, *Hedlund* (S – holotype!).

Lecidea triseptatuloides Harm. in *Bull. Séanc. Soc. Sci. Nancy* II, **33**: 64 (1899). – *Bacidia triseptatuloides* (Harm.) Zahlbr., *Cat. lich. univ.* **4**: 161 (1926). Type: France, Moselle, Bitche, on *Pinus* bark, xii 1893, *Abbé Kieffer* (ANGUC – holotype!).

Micarea violacea f. *exigua* Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 81, 91 (1892); *nom. inval.* (Art. 26).

Notes: (i) *'saxigena'*. This epithet has been applied at intra-specific levels to saxicolous forms of *M. lignaria* and *M. peliocarpa.* Its first valid publication was by Hepp (loc. cit.) as '*Biatora lignaria* (Ach.) var. *saxigena* (Leight) Hepp' with '*Lecidea milliaria* (Fries) v. *saxigena,* Leight *Lich. Brit. Exs.* 210' given as a synonym. All examples seen by me of Leighton *Lich. Brit.* 210 (issued in 1856) are *M. lignaria*; whereas all examples of Hepp *Flecht. Eur.* 510 are *M. peliocarpa*. Hepp's illustration and description of spores are more applicable to *M. peliocarpa* than *M. lignaria*. The original valid introduction of the epithet '*saxigena*' should, therefore, be typified on an example of Hepp *Fl. Eur.* 510 and attributed to Hepp alone.

Theoretically '*saxigena* Leighton' could have been validated for saxicolous forms of *M. lignaria* by providing a description, excluding other names or specimens that would render it superfluous, and avoiding homonymy with previous combinations of '*saxigena* Hepp'; but I have not found such a case in the literature.

(ii) '*trisepta*'. This epithet first appeared as '*Biatora trisepta* Naeg. mss. ex Dr Hepp' in the protologue of

Patellaria salevensis Müll. Arg. (= *Bacidia salevensis* (Müll. Arg.) Zahlbr.). Müller presumably regarded Naegeli's manuscript name as a synonym of his new species. *B. salevensis* (type in BM!) is a limestone species and is not a *Micarea*. As indicated by James (1965: 103) the first legitimate publication of the epithet '*trisepta*' for a *Bacidia*-like species is that by Hellbom (*loc. cit.*). By including the epithet in *Bilimbia* as '*B. trisepta* (Naeg.)', Hellbom was clearly using it in its traditional sense and not introducing it as an entirely new name. There is no indication that any of the authors using the epithet '*trisepta* Naeg.' had seen Naegeli's original material, and no such material has been found amongst Hepp's collections at BM. Because the original material is probably no longer in existence, neotypification is required. The epithet '*trisepta*' has been a long source of confusion, being used by various authors for several species, especially *Micarea lignaria, M. melaena, M. nitschkeana, M. peliocarpa,* and *M. ternaria*. However, it is clear from the descriptions and cited specimens in Stizenberger (*loc. cit.*), Bausch (*loc. cit.*), Hedlund (1892), and Vainio (1922) that the epithet '*trisepta*' has most commonly been applied to the species now called *Micarea peliocarpa*. Because '*trisepta*' first appeared in the protologue of a saxicolous species the neotype chosen is an example of Hepp *Flecht. Eur.* 510 which was cited under, or in connection with, '*trisepta*' in the treatments of Stizenberger, Bauch, Hedlund, and Vainio.

Thallus effuse, sometimes partly endocuticular, endophloeodal or endoxylic, more usually developed on the surface of the substratum as rounded, shallow-convex, hemispherical, or ± globose areolae. Areolae scattered or more usually ± continguous, greenish white, or grey-white to blue-grey, occasionally becoming dark grey, often dark coloured on upper surface but pale and greenish white below, matt or slightly glossy, *c.* 40–200 μm diam. Areolae in section, ecorticate but with an amorphous hyaline covering layer *c.* 2–5 μm thick; outermost hyphae often with grey-green to blue-green walls, K−, HNO_3+ red. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia scattered or more usually crowded and often contiguous, adnate, plane to convex, sometimes becoming tuberculate; sometimes with an indistinct margin that is flush with the level of the disc; rarely (as in shaded corticolous forms) whitish or ivory-white, usually pale lead-grey to grey-black, sometimes grey-brown, often whitish or paler at the margin; (0·12–)0·14–0·4 (–0·6) mm diam, or to 1 mm when tuberculate. Disc finely roughened, matt, or slightly glossy (when black); margin (when evident) smooth and often more glossy than the disc. *Hymenium* 40–55 μm tall, usually olive-green or aeruginose (K−, HNO_3+ red) in upper part and ± hyaline below; in dark coloured apothecia the green pigment often occurs as vertical streaks through the hymenium. *Asci* clavate *c.* 40–55×12–17 μm. *Spores* fusiform, clavate-fusiform, or oblong-fusiform, often slightly curved, (1–)3(–5)-septate, (11–)15–23(–24)×3–5(–6) μm. *Paraphyses* numerous, branched, often anastomosing, 1–1·5 μm wide; apices often more richly branched and entangled, often slightly incrassate to *c.* 1·8 μm, or to 2·5 μm due to thickening by green pigment. *Hypothecium c.* 40–70 μm tall, hyaline or dilute straw; hyphae interwoven, *c.* 1–1·7 μm wide; ascogenous hyphae with swollen cells *c.* 2–4 μm wide. *Excipulum* well developed, hyaline, or dilute straw in part, of richly branched and anastomosing, radiating hyphae *c.* 1–1·5 μm.

Pycnidia frequently present (especially on bark or lignum), of two types: (a) immersed in areolae, white or greenish around the ostiole, 140–200 μm diam, ostiole often widely gaping; *conidia* (*macroconidia*) markedly curved and often sigmoid, often faintly 1–5-septate, 21–40(–50)×1–1·5 μm; (b) ± sessile, white, 50–80 μm diam, ostioles not, or only slightly, gaping; *conidia* (*microconidia*) narrowly fusiform-cylindrical, (5–)6–7(–7·7)×0·4–0·7 μm.

Chemistry: Thallus and whitish apothecia K−, C+ red, PD−; apothecia in section C+ orange-red; t.l.c.: gyrophoric acid.

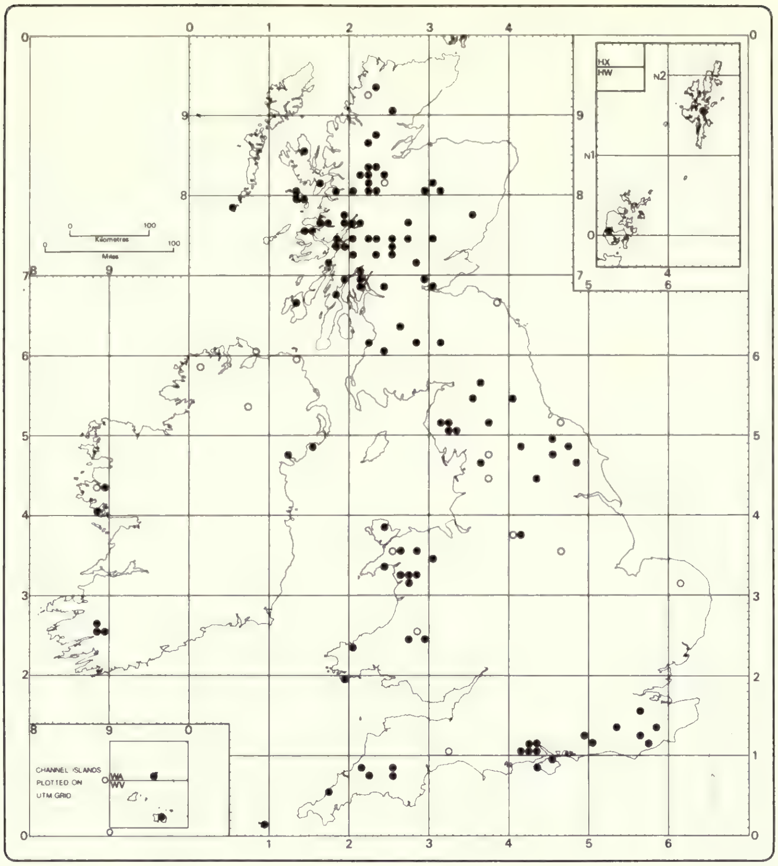
Observations: M. peliocarpa occurs in a wide range of habitats and is concurrently variable, especially regarding the colour of its apothecia and thallus. This variation is considered to be phenotypic, being due to the amount of green pigment produced in the hymenium and near the surface of the thallus in response to environmental factors, particularly light. When on the bark of old trees in sheltered woodland the apothecia are often very pale to blue-grey, more scattered than usual, and accompanied by numerous pycnidia; such forms are frequent in the ancient woodlands of the New Forest, Hampshire. There is some variation as to the production of areolae, these being often poorly developed or even absent when on cortex or lignum, and usually abundant and well developed in more exposed situations on mossy rocks and peaty debris.

M. peliocarpa is most closely related to *M. alabastrites* and *M. cinerea* (see under the former for further discussion). Apart from these two species, *M. peliocarpa* is most often confused with *M. lignaria* (*q.v.*) especially when occurring in exposed habitats where its apothecia may be black and markedly convex. Similarly, confusion could occur with the rare *M. ternaria* (*q.v.*), which like *M. peliocarpa* has rather flattened apothecia (in section) with a well developed excipulum. When fertile, *M. leprosula* has apothecia very like those of *M. peliocarpa*, but its thallus is composed of fragile areolae that readily dissolve into soredia and contains argopsin (PD+ red) as well as gyrophoric acid. In certain habitats, such as the stems of old shrubs (e.g. *Calluna, Erica,* and *Ulex*), *M. peliocarpa* could be mistaken for *M. nitschkeana* although the latter has an olivaceous, K+ violet pigment in the hymenium, pycnidial walls and thallus, and smaller spores. Specimens collected from *Xanthorion* communities and attributed to *M. peliocarpa* (or one of its synonyms) are mostly referable to *Bacidia naegelii*, which has simple paraphyses with markedly swollen apices, an excipulum of coherent hyphae (in K), and a very different thallus structure.

Habitat and distribution: M. peliocarpa is rather catholic in its choice of habitat. As an epiphyte on bark (or on bryophytes thereon) it is mostly commonly found on mature *Quercus*, but has also been collected from *Alnus, Betula, Fagus, Fraxinus, Ilex, Salix, Larix, Pinus, Juniperus, Calluna, Erica,* and *Ulex*. It has a preference for trunks and main stems rather than small twigs and branches. Amongst the British collections associated lichens on bark include *Arthonia spadicea, Biatorina atropurpurea, 'Botrydina vulgaris', Cladonia* spp., *Hypogymnia physodes, Lecanora pallida, L. symmicta* agg., *Lecidea icmalea, Leparia incana* agg., *Micarea alabastrites, Micarea cinerea, Normandina pulchella, Ochrolechia androgyna, Parmelia saxatilis, Parmeliella jamesii, Pertusaria hymenea, Phyllopsora rosei, Platismatia glauca, Stenocybe septata* and *Trapelia* sp. In the north and west of Britain it is frequently encountered on the lignum of fallen trunks and large branches (especially conifers), accompanied by such species as *Lecidea granulosa* agg., *L. turgidula, Micarea denigrata, M. lignaria* (including var. *endoleuca*), *Mycoblastus sterilis, Ptychographa xylographoides, Xylographa abietina,* and *X. vitiligo*. In the same areas it is often common on peaty soil, and on moribund bryophytes or peaty debris on old walls, boulders and rock faces, preferring rather more sheltered conditions than *M. lignaria,* with which it is easily confused in the field. Furthermore, it is not found at such high altitudes as attained by that species, and all British collections seem to have been made at below 500 m. Associated species in these habitats include *Cladonia crispata, C. coccifera, C. squamosa, C. uncialis, Coelocaulon aculeatum* s. lat., *Hypogymnia physodes, Lecidea icmalea, Micarea leprosula, Ochrolechia androgyna, Parmelia saxatilis,* and *Platismatia glauca*. It is less frequently found growing directly on rock, and records from Britain indicate that it is able to do so only in rather dry situations. Such occurrences are mostly in the rather low rainfall districts of, for example, Durham, east Yorkshire and Sussex; accompanying species noted include *Baeomyces rufus, Cystocoleus ebeneus, Lecidea granulosa* agg., *L. icmalea, Lecanora polytropa, Lepraria incana* agg., *Parmeliopsis ambigua, Trapelia coarctata,* and *T. involuta*.

M. peliocarpa is widely distributed in Britain but is most common in the west and in upland districts (but at low altitudes). This pattern is reflected in Europe as a whole, and it is apparently common in countries along the Atlantic seaboard and on the Atlantic islands including Iceland, the Azores, and Canary Islands. In central and eastern Europe it is found mainly in mountainous districts. Northwards it extends to just beyond the Arctic Circle, but I do not know of its occurrence in the high arctic. From outside Europe I have seen material from eastern Canada and north-eastern USA, and from New Zealand.

Exsiccata: Anzi *Lich. Sondr.* 170A (UPS). Arnold *Lich. Exs.* 167A, B (BM ex K, M), 837, 1051 (BM ex K). Arnold *Lich. Mon.* 118 (BM ex K), 269, 357, 482 (BM ex K, MANCH). Hepp *Flecht. Eur.* 284 (E, M), 285 (E, L, M), 510 (E, M). Hepp *Zür.* 206 (BERN). Körber *Lich. Sel.Germ.* 133A, B (M). *Krypt. Exs. Vindob.* 165 (BM). Larb. *Lich. Herb.* 347 (BM). Leighton *Lich. Brit.* 238 *p.p.* (BM, DBN, FRS). Lojka *Lich. Hung.* 134 (BM ex K). Malme *Lich. Suec.* 169 (S). Räsänen *Lichenoth. Fenn.* 343 (BM). Vězda *Lich. Sel.* 1342, 1380 (BM). Zwackh. *Lich. Exs.* 276, 897 (UPS).



Map 17 *Micarea peliocarpa* ● 1950 onwards ○ Before 1950

34. **Micarea prasina** Fr.
(Figs 1D, 26–27, 49, 53–54; Maps 18–20)

Syst. orb.: 256–7 (Dec. 1825). – *Biatora prasina* Fr., *Stirp. agri femsion.*: 36 (June 1825), *nom. illeg.* (Art. 63). – *Biatora prasina* (Fr.) Trevisan, *Linnaea* **28**: 288 (1856), nec Tuck. & Mont., in Mont. (1857). – *Catillaria prasina* (Fr.) Th. Fr., *Lich. Scand.* **2**: 572 (1874). See note (i) below and note on *Sporacestra* under 'Excluded taxa'.

Biatora micrococca Körber, *Parerg. lich.*: 155 (1860). – *Catillaria micrococca* (Körber) Th. Fr., *Lich. Scand.* **2**: 571 (1874). – *Micarea prasina* f. *micrococca* (Körber) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 77, 87 (1892). – *Micarea micrococca* (Körber) H. Gams, *Kleine Kryptfl.* **3**: 67 (1967); *comb. inval.* (Art. 33.2). Type: Germany, Baden-Württemberg, 'in regno Wurtembergico', on *Pinus* bark, 1862, *K. A. Kemmler,* Körber Lich. Sel. germ. 250 (L 910, 139–1361–neotype! [t.l.c.: 'prasina-unknown A']). See note (ii) below.

Lecidea subviridescens Nyl. in *Flora, Jena* **51**: 474 (1868). – *Micarea subviridescens* (Nyl.) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 77, 87 (1892). – *Bacidia subviridescens* (Nyl.) Zahlbr., *Cat. lich. univ.* **4**: 154 (1926). Type: Channel Islands, Jersey, Boulay Bay, on coastal turf and soil, 1868, *C. Larbalestier* (H-NYL 19056 [as '*subvirescens*'] – lectotype!; BM – isolectotype! [t.l.c.: 'prasina unknown C']; BM – topotypes!). See note (iii) below.

Lecidea prasiniza Nyl. in *Flora, Jena* **57**: 312 (1874). – *Micarea prasina* f. *byssacea* subf. *prasiniza* (Nyl.) Th. Fr. *in* Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 77 (1892). Type: Finland, Tavastia australis, Padasjoki, Nyystölä, on *Alnus,* 1872, *E. A. Lang [Vainio]* (H-NYL 21604 – lectotype!, H – isolectotype!). [material insufficient for t.l.c.].

Lecidea sordidescens Nyl. in *Flora, Jena* **57**: 312 (1874). – *Lecidea erysiboides* f. *sordidescens* Nyl. *in* Norrlin in *Not. Sällsk. Fauna Fl. fenn. Förh.* **11**: 188 (1870); *nom nudum* (Art. 32). – *Catillaria prasina* var. *byssacea* f. *sordidescens* (Nyl.) Blomb. & Forss., *Enum. Pl. Scand.*: 91 (1880). – *Micarea prasina* f. *byssacea* subf. *sordidescens* (Nyl.) Th. Fr. *in* Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 77 (1892). – *Lecidea byssacea* var. *sordidescens* (Nyl.) Vainio in *Természetr. Fuz.* **22**: 320 (1899). – *Catillaria prasina* var. *sordidescens* (Nyl.) Lettau in *Hedwigia* **52**: 136 (1912). – *Micarea prasina* var. *sordidescens* (Nyl.) Brodo in *Bull. N. Y. St. Mus. Sci. Serv.* **410**: 152 (1968). Type: Switzerland, Zürich, 'An faulen Fichten-Strunken Z. H.', *Hepp, Flecht. Eur.* 278 (E – lectotype! [t.l.c.: 'prasina-unknown B']; isolectotypes: BM (boxed set)! [t.l.c.: 'prasina-unknown B'], H-NYL 21632 [fragment]!, M!). See note (iv) below.

Lecidea prasiniza var. *prasinoleuca* Nyl. in *Flora, Jena* **64**: 7 (1881). Type: Germany, Baden-Württemberg, Heidelberg, Königstuhle, on *Picea abies*, ix 1880, *Zwackh,* Lich. Exs. 593a (H-NYL 21601 – lectotype! [t.l.c.: 'prasina-unknown A']). See note (v) below.

Catillaria micrococca f. *glebosula* Erichsen in *Annls mycol.* **36**: 139 (1938). Type: Germany, Schleswig-Holstein, Eiderstedt, Ording, at base of *Betula,* 4 viii 1913, *C. F. E. Erichsen* (HBG – holotype! [t.l.c.: 'prasina-unknown B'].

Catillaria micrococca var. *discrepans* Erichsen in *Annls mycol.* **36**: 139 (1938). Type: Denmark, Jylland, Åbenrå (Apenrade), on smooth bark of *Alnus* in a valley near Elisenlund, 3 ix 1913, *C. F. E. Erichsen* (HBG – holotype!). [material insufficient for t.l.c.].

Catillaria prasina var. *occulta* Erichsen in *Annls mycol.* **36**: 140 (1938). Type: Germany, Schleswig-Holstein, Ratzeburg, in the wood 'Bak', on ± smooth bark of *Alnus,* 21 iii 1918, *C. F. E. Erichsen* (HBG – holotype!). [material insufficient for t.l.c.].

Lecidea declivitatum Erichsen in *Mitt. Inst. allg. Bot. Hamb.* **10**: 408 (1939). Type: Germany, Schleswig-Holstein, 'Krs Eutin: an der Boschung eines Waldwegs an der Nordwest-Seite des Ugleisees', 5 vi 1914, *C. F. E. Erichsen* (HBG – holotype! [t.l.c.: 'prasina-unknown C']).

Micarea polytrichi Poelt & Döbb. in *Bot. Jb.* **96**: 343 (1975). Type: Austria, Steiermark, Grazer Bergland, a little north of Maria Trost near the Wenisbucher Strasse, *c.* 460 m, on *Polytrichum formosum* on shady side of a narrow gorge, 30 iii 1974, *J. Poelt* (GZU – holotype!) [material insufficient for t.l.c.].

Catillaria prasina α *laeta* Th. Fr., *Lich. Scand.* **2**: 573 (1874); *nom. inval.* (Art. 26).

?*Biatora byssacea* Zwackh in *Flora, Jena* **45**: 510 (1862), non Hampe in *Linnaea* 25: 709 (1852). Type: Germany, Heidelberg, 'Königsstuhle', on bark of old *Quercus,* ? *Zwackh* (not traced). See note (vi) below.

?*Catillaria melanobola* f. *biseptata* B. de Lesd., *Rech. Lich. Dunkerque*: 198 (1910). Type: France, Nord, Dunkerque, St Pol, on a piece of leather in dunes, *B. de Lesdain* (not seen).

?*Catillaria melanobola* f. *nigra* B. de Lesd., *Rech. Lich. Dunkerque*: 199 (1910). Type: France, Nord, Dunkerque, lignum of hollow *Salix, B. de Lesdain* (not seen).

Notes: (i) *Biatora prasina* Fr. (June 1825) is superfluous because the protologue includes the sentence: 'Crusta est Byss. botryoides Linn!'. *Byssus botryoides* L. is a valid name (*Sp. pl.* **2**: 1169 (1753)) but the material in the Linnaean herbarium (LINN) is a specimen (1278.16) labelled by Ehrhart; it is an alga and bears a determination label: '*Protococcus viridis* Ag. Determined by Francis Drouet iv. 1950'. In the protologue of *Micarea* and *M. prasina,* Fries (Dec. 1825) makes a less dogmatic statement, merely indicating that when sterile *M. prasina* is indistinguishable from *B. botryoides*; *M. prasina* is, thereby, not rendered superfluous.

(ii) I have seen two specimens named by Körber and collected from 'Würtemberg' by Kemmler: an undated specimen in WRSL and possibly part of the original gathering, and a later specimen issued in Körber's exsiccata. The first specimen would have to be completely destroyed for t.l.c. analysis, whereas the exsiccate specimen is larger and was found to contain 'prasina-unknown A', and it is this specimen that I have chosen for typification. If future studies require this chemical race to be recognized at specific rank, then '*micrococca*' is the earliest available epithet.

(iii) *L. subviridescens* is the earliest name for the chemical race with 'prasina-unknown C'.

(iv) Although Nylander (1874) did not provide a description, he validated *L. sordidescens* by referring to it Hepp *Flecht. Eur.* 278; the printed label for this exsiccatum includes a short description and a drawing of spores.

(v) If the chemical race containing 'prasina-unknown A' were to be awarded varietal rank, then this name provides the earliest available epithet, provided that '*byssacea*' is not available; see also note (vi).

(vi) I have not seen a holotype specimen or any material suitable for the lectotypification of *Biatora byssacea* Zwackh. A neotype has not been selected because this name is a later homonym of *B. byssacea* Hampe. Hampe's name was given to a specimen collected by Charles Stuart in Tasmania, and the protologue ends with 'an status degenerans'. *Biatora byssacea* Hampe is included by Zahlbruckner (*Cat. lich. univ.* **3**: 897) in a list of excluded and dubious names and is not accorded a catalogue number; the type material has not been located in BM but it could be elsewhere (? G). Under the taxonomic arrangement given here Zwackh's epithet is of no consequence. If the chemical races of *M. prasina* were to be awarded varietal status, then under the provisions of Article 72 the name '*Catillaria prasina* β. [var.] *byssacea* Th. Fr. (1874)' could become important and require typification. If this name was typified with a specimen containing 'prasina unknown A' then it would be the earliest available name at that rank.

Thallus effuse and often wide-spreading, very variable in colour, pale fawn (dry shaded situations), light green, pale to dark grey-green (often with glaucous hue), or olivaceous to olive-black, often appearing ± gelatinous when moist, composed of small ± globose granules (goniocysts). Goniocysts *c.* 12–40(–60) μm diam, thinly scattered, or vertically proliferating to give the thallus a soft isidiose appearance, or densely aggregated to form a thick granular crust up to 200 μm deep. Goniocysts ecorticate, often with shortly protruding hyphal filaments; outermost hyphae of superficial goniocysts sometimes surrounded by greenish, K+ violet pigment. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia usually numerous but sometimes few or absent, immarginate, sometimes adnate and shallow-convex, but more usually becoming markedly convex, subglobose or tuberculate; colour variable, whitish or pallid ('*micrococca*' shade-forms), pale to dark grey, brownish grey, or grey-black, matt; 0·1–0·4 mm diam, or to 0·6 mm when tuberculate. *Hymenium* 28–45(–52) μm tall, hyaline or dilute dull straw, but more usually dull olivaceous, especially in the upper part (but coloured portion not sharply delimited) or in vertical streaks; pigment K+ violet, HNO_3+ red, confined to gel-matrix. *Asci* clavate or cylindrical-clavate, 26–40(–50)×8–12 μm. *Spores* ovoid-ellipsoid, ovoid, ovoid-oblong or oblong, 0–1(–3)-septate; when 1-septate the lower cell is slightly longer and narrower than the upper, and there is often a slight constriction at the septum; variable in size, in range 8–14(–17)×2·3–4(–5) μm. *Paraphyses* rather numerous, branched and anastomozing, 0·5–1 μm wide; apical parts often wider, to 1·5 μm, but not thickened by pigment; epithecial pigment confined to surrounding gel matrix. *Hypothecium c.* 40–170 μm tall, hyaline to dilute dull yellowish; hyphae interwoven, some becoming vertically orientated towards the hymenium, *c.* 0·7–1·3 μm wide; ascogenous hyphae with swollen cells, *c.* 2–4 μm wide. *Excipulum* poorly developed, sometimes evident as a narrow, hyaline or dilute olivaceous-straw (K+ violet), non-amyloid, reflexed zone; hyphae radiating, branched and anastomosing, *c.* 0·7–1 μm wide.

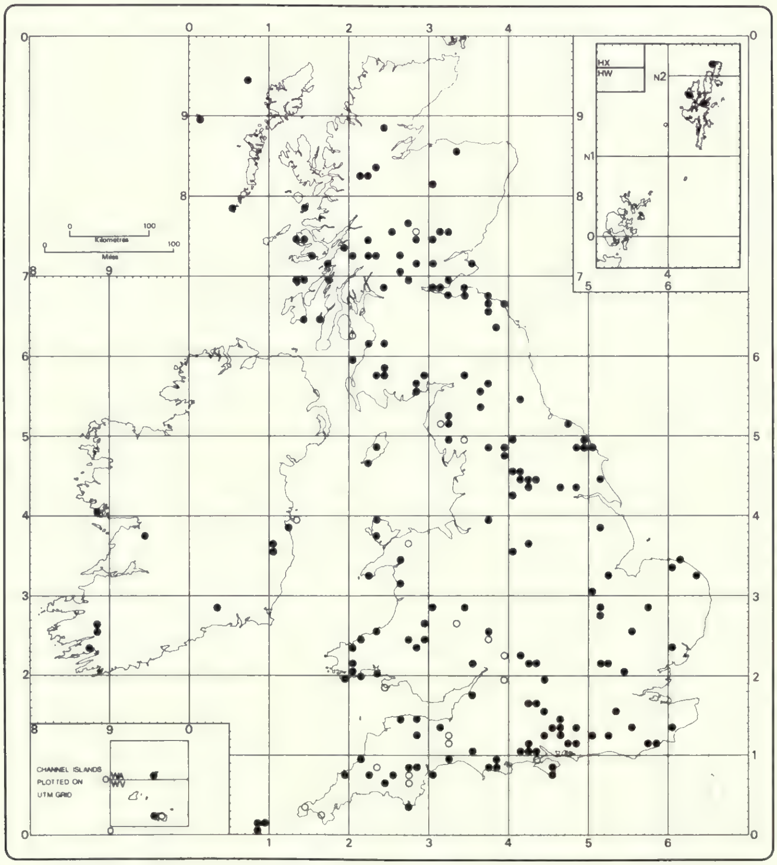
Pycnidia often present but usually inconspicuous, white, or upper part around the ostiole grey (due to olivaceous, K+ violet pigment), immersed to sessile (never distinctly stalked), of two types: (a) *c.* 50–120 μm diam, emergent to sessile, ostiole sometimes gaping; *conidia* (*mesoconidia*) ± cylindrical or narrowly obpyriform, often biguttulate and slightly constricted near the middle, (3·5–)4–6×1·2–1·7 μm; (b) *c.* 30–60(–100) μm, usually immersed in surrounding goniocysts, ostiole rarely gaping; *conidia* (*microconidia*) cylindrical or narrowly fusiform, (5–)5·5–8×0·7–1 μm.

Chemistry: All parts K−, C− (but olivaceous pigment C+ violet, never red), PD−; t.l.c.: specimens have one of three unknowns ('prasina unknown A', 'B', or 'C'; see p. 87); trace amounts of gyrophoric acid sometimes detected, possibly due to contamination by intimately associated species such as *Lecidea icmalea* and *L. granulosa* agg.

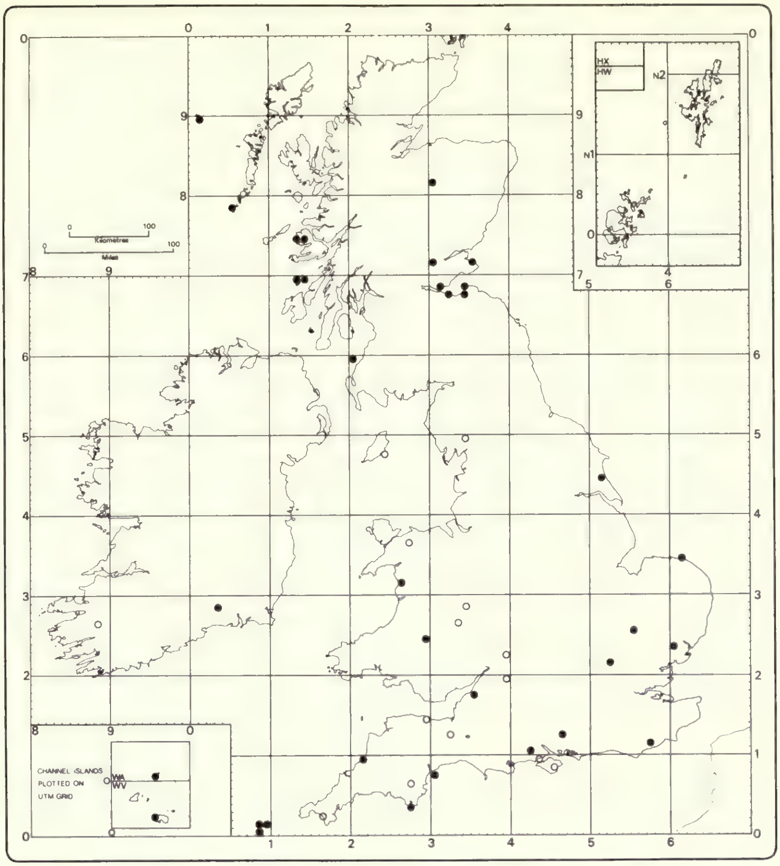
Observations: Micarea prasina is the commonest and most variable member of the genus. However, it is one of the few European species whose thallus is composed of minute discrete granules (goniocysts). Two other species with a similar thallus are: *M. hedlundii* (*q.v.*) with a K+ red oily substance in the goniocysts and conspicuous tomentose, brown, stalked pycnidia; and *M. melanobola* which has a sharply delimited epithecium (pigment closely adhering to apices of the paraphyses) and shorter microconidia. Both of these species appear to be very rare. A comparison of the diagnostic features of *M. melanobola, M. prasina* and *M. misella* are given in Table 6.

Diminutive forms of *M. prasina* with small pallid apothecia and a scanty thallus have sometimes been regarded as a distinct species ('*Catillaria micrococca*'). Such forms have the same basic thallus structure, spores, paraphyses, anamorphs and chemistry (with either 'prasina unknown A' or 'B') as more typical forms (with coloured apothecia and more robust thallus), and I have seen intermediates on many occasions. The '*micrococca*' forms are found in heavily shaded situations (e.g. tree trunks in dense conifer plantations, and trunks of understory trees or shrubs) and I consider their diminutive stature and lack of pigmentation to be a phenotypic response to low light intensities. The specimens described as *Micarea polytrichi* are similarly diminished forms, in this case overgrowing mosses (mainly *Polytrichum* spp.) by woodland roads.

European populations of *M. prasina* have been found to be represented by three chemical races, each with one of three distinctive, but as yet unidentified, substances (see p. 87). During the course of the present study I have been tempted to recognize the chemical races as formal varieties. However I defer from doing so at this time because: (a) the chemical structure and biogenetic relationships between the three substances is not yet known; (b) the three chemical races do not consistently correlate to any clear differences in morphology; (c) the correlations between chemistry and distribution and (or) ecology are as yet uncertain. In the British Isles (at least) the race containing the 'unknown A' is by far the commonest and is a ubiquitous coloniser of trees and shrubs in all types of woodland (including young conifer plantations), occurring on tree boles, bark and lignum of fallen trees and stumps, and fallen sticks; it also occurs on shaded mossy turf on the ground and amongst rocks (usually with an east- or north-facing aspect) in maritime situations. The race containing 'unknown B' has a more restricted ecology and is mainly found in old woodland situations (including the native pine-woods), growing on the rather dry lignum or old bark of large stumps or fallen trunks; it has not been found on coastal turf or rocks. Specimens of this race tend to have a thick, pale grey (often abrading to greenish



Map 18 *Micarea prasina sensu lato* ● 1950 onwards ○ Before 1950

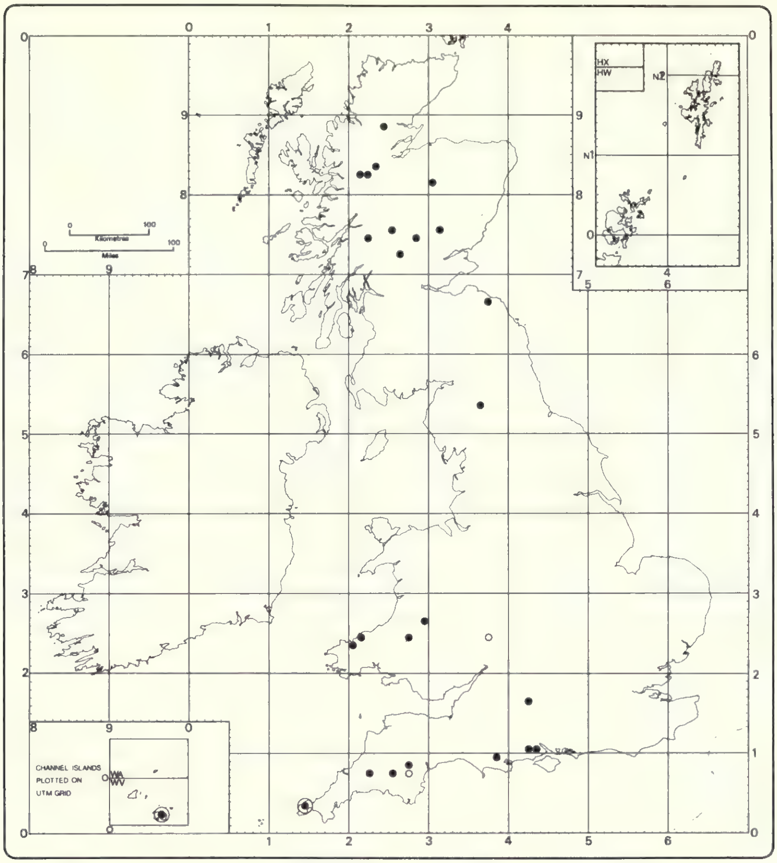


Map 19 *Micarea prasina* substance A ● 1950 onwards ○ Before 1950

white) thallus, but equivalent morphological forms containing 'unknown A' are sometimes encountered. Specimens containing 'unknown C' are exceedingly rare and are known only from coastal turf in south-west England and the Channel Islands, and on argillaceous soil on a bank by a woodland path in south-eastern Schleswig-Holstein. The above ecological and phytogeographical tendencies require to be more thoroughly tested throughout the range of *M. prasina*, and it is possible that a good case for the taxonomic recognition of these races as varieties, subspecies, or even species could be made.

The type material of *Lecidea subviridescens* contains 'unknown C' and has spores that are at the high end of the overall size range for *M. prasina s. ampl.* (10–18×4–5·5 μm) and some with two or three septa. However the very large 2–3-septate spores are always old with secondarily thickened walls, and similar spores are sometimes encountered in other *Micarea* species that have predominantly 1-septate spores. Furthermore, similarly large, 2–3-septate spores have been found in some coastal specimens containing 'unknown A' and in some inland, lignicolous specimens containing 'unknown B'. Although I regarded '*subviridescens*' as a separate species in the recent British checklist (Hawksworth *et al.*, 1980: 62), I now believe it should be subsumed under *M. prasina* pending further studies as intimated in the preceding paragraph.

Habitat and distribution (see also 'observations'): As an epiphyte on trees or shrubs *M. prasina* has been found on a wide range of phorophytes; in Britain these include *Acer, Alnus, Betula, Castanea, Corylus, Fagus, Fraxinus, Metrosideros, Quercus, Salix, Sambucus, Sorbus, Ulmus, Calluna, Erica, Rhododendron, Vaccinium, Sarothamnus, Ulex, Abies, Larix, Picea, Pinus, Pseudotsuga,* and *Juniperus*. It occurs on the bark or lignum (old dried wounds, etc.) of



Map 20 *Micarea prasina* substance B ● 1950 onwards ○ Before 1950 substance C ◉ Before 1950

shaded trunks or main stems, but also on low (shaded) branches, fallen debris (especially in conifer plantations) and stumps. It is usually found in woodlands but sometimes occurs in sheltered niches in situations, e.g. bases of *Ulex* stems in more open, exposed hillside gorse-scrub.

The phytosociological affinities of *M. prasina* are various and difficult to define. When on the bark of deciduous trees it sometimes occurs in shaded facies of communities belonging to the *Lobarion pulmonariae, Parmelietum revolutae,* and the *Pseudevernietum furfuraceae*. It is frequently found in small bark crevices amongst ± smooth areas of bark which are colonized by communities of the *Graphidetum scriptae, Pyrenuletum nitidae,* and *Lecanoretum subfuscae*. When occurring in such situations as the shaded trunks of young conifers or shrubs *M. prasina* often exists as ± pure stands; more detailed phytosociological studies may well lead to the formal syntaxonomic recognition of such communities. From amongst the British collections in E the associated species of *M. prasina* on the bark of deciduous trees include *Arthonia spadicea, Bacidia vezdae, Chrysothrix candelaris, Cladonia coniocraea, Dimerella diluta, Evernia prunastri, Graphis elegans, Gyalideopsis anastomosans, Hypogymnia physodes, Lecidea icmalea, Lepraria incana, Ochrolechia androgyna, Opegrapha vulgata, Pachyphiale cornea, Parmelia glabratula, P. sulcata, Pertusaria multipuncta, Thelotrema lepadinum, Trapelia corticola, Dicranoweissia cirrata, Frullania* spp., *Hypnum cupressiforme, Lejeunea ulicina,* and *Metzgeria furcata*.

When on lignum its affinities are similarly difficult to define but it is often found in more sheltered or shaded (humid) niches adjacent to communities of the *Calicietum abietini, Cladonietum coniocraeae, Lecideetum ostreatae,* and *Parmeliopsidetum ambiguae*.

Species associated with *M. prasina* on the lignum of fallen trunks and large stumps in the British Isles include *Bryoria fuscescens, Chaenotheca ferruginea, Chaenothecopsis* spp., *Cladonia chlorophaea* agg., *C. macilenta, C. ochrochlora, Hypocenomyce scalaris, Hypogymnia physodes, Lecanactis abietina, Lecidea aeruginosa, L. icmalea, Micarea adnata, M. melaena,* and *Platismatia glauca*.

In coastal districts *M. prasina* is often found on plant debris, soil or moribund bryophytes in rock crevices or on ledges in sheltered gullies, and sometimes it occurs on the ground growing over plant debris or old *Armeria* tussocks, etc. Such habitats are usually sheltered and (or) with a north- to east-facing aspect. Associated lichens are few, but include *Cladonia* spp., *Lecidea granulosa, L. icmalea,* and *Lepraria incana* agg. Finds of *M. prasina* growing directly on rock are very rare, but I have seen a few collections made from sandstone rocks in woodlands (from east Sussex and north-east Yorkshire).

M. prasina is still to be found close to the centres of large conurbations and cities (e.g. Bristol, Edinburgh, London, and the West Yorkshire conurbation), and its persistence is probably due more to its ability to avoid, rather than tolerate, the direct effects of air pollutants such as sulphur dioxide and its derivatives. It naturally favours substrata with a low pH and is able to grow in very sheltered and shaded situations where more light demanding pollution resistant species (especially *Lecanora conizaeoides*) are at a competitive disadvantage.

M. prasina s. ampl. is widely distributed in the British Isles and much of Europe. In Scandinavia it occurs northwards to at least *c.* 67°N. It may be rare in districts adjoining the Mediterranean Sea, but those areas are mostly poorly known lichenologically, and I have seen one collection from Toscana (northern Italy). *M. prasina* is present in Macaronesia (Azores and Canary Islands) and I have seen collections of it from several states in the U.S.A. (Georgia, Maryland, Massachusetts, Michigan, and Wisconsin). In addition I have seen several collections from South America and Australisia which come close to *M. prasina,* but these require more critical study and will be treated in a later publication.

Exsiccata. Containing 'prasina unknown A': Arnold *Lich. Exs.* 1122, 1472 (BM ex K, M). Körber *Lich. Sel. Germ.* 250 (L). Lojka *Lich. Univ.* 29 (BM ex K, M), 30 (BM ex K). Malme *Lich. Suec.* 23 (M, S). Rabenh. *Lich. Eur.* 676 (BM, BM ex K, M, WRSL). Räsänen *Lich. Fenn.* 651 (BM, BM ex K, M), 652 (BM, BM ex K). Vězda *Lich. Sel.* 90 (BM, M), 1467 (BM). Zwackh. *Lich. Exs.* 593A (H-NYL 21601). *Containing 'prasina unknown B':* Arnold *Lich. Exs.* 280C (BM, GZU, M, WRSL). Cumm. *Dec. N. Am. Lich.* I. 355 (BM, WIS). Hepp *Flecht. Eur.* 278 (BM, E, M, WRSL). Lojka *Lich. Univ.* 31 (BM ex K, M). *Chemistry not tested:* Arnold *Lich. Exs.* 279 (WRSL), 280A (BM, BM ex K, M), 280B (BM ex K, M). Arnold *Lich. Mon.* 243 (UPS), 245 (BM ex K, M). Hepp *Zür.* 224 (BERN). Kuták *Lich. Bohem.* 310 (O). Magnusson *Lich. Sel. Scand.* 134 (BM). Malme *Lich. Suec.* 24 (M, S). Rabenh. *Lich. Eur.* 733 (H). Räsänen *Lich. Fenn.* 653 (LD). Schaerer *Lich. Helv.* 196 *p.p.* (BM ex K, M). Vězda *Lich. Sel.* 1595 (BM, GZU, M). Zahlbr. *Lich. Rar.* 175 (BM). Zwackh. *Lich. Exs.* 416 (UPS), 591A (H-NYL 21598), 591B (H-NYL 21594, 21599), 592A (UPS), 592B (M, UPS), 592C (UPS), 592D (M, UPS), 592E (UPS), 593B (H-NYL 21600), 593C (H-NYL 21595), 656 (UPS).

35. **Micarea pycnidiophora** Coppins & P. James
(Fig. 28: Map 21)

in *Lichenologist* **11**: 153 (1979). Type: England, South Hampshire, New Forest, near Cadnam, Shave Wood, 45 m, on bark of *Fagus,* 5 xi 1972, *B. J. Coppins & F. Rose* (E – holotype!; BM – isotype!).

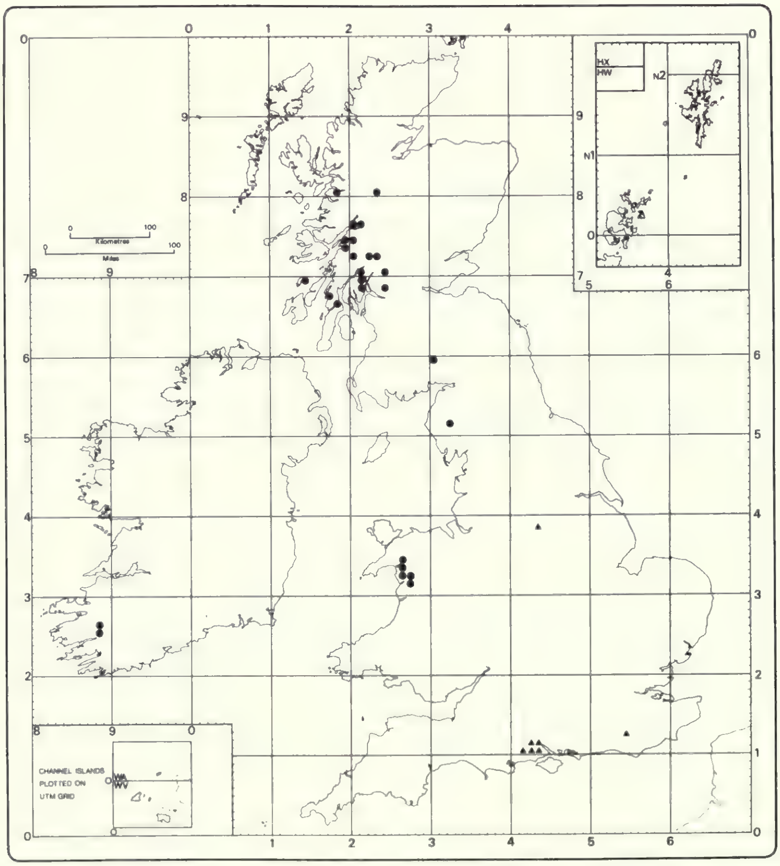
Thallus corticolous, often overgrowing moribund thalli of bryophytes and other lichens; effuse, often wide-spreading, thin, uneven, composed of scattered to confluent areolae arising from a thin varnish-like prothallus. Areolae flattened to convex-hemispherical, grey-green or dull green, *c.* 40–100 μm diam; in section, without a distinct cortex or hyaline amorphous covering layer. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia usually few or absent but sometimes abundant, immarginate, convex-hemispherical to globose, often tuberculate, ivory-white to pallid, translucent when moist, surface matt, 0·1–0·3 mm diam. *Hymenium* 35–50 μm, hyaline. *Asci* clavate, 30–35 × 10–12 μm. *Spores* ± straight and vertically aligned in the ascus (never tightly spiralled), shortly acicular, upper end usually broader and more obtuse than the lower end, usually slightly curved, 3–7-septate, (14–)21–34×2–2·5(–2·7) μm. *Paraphyses* numerous, branched and anastomosing, *c.* 1–1·5 μm, not swollen at apices. *Hypothecium* 20–80 μm tall, hyaline; hyphae interwoven, but becoming vertically orientated towards the hymenium, *c.* 1–1·5 μm wide; ascogenous hyphae with swollen cells, *c.* 2–4 μm wide. *Excipulum* poorly developed (*c.* 10 μm wide); hyphae radiating, branched and anastomosing, *c.* 1 μm wide.

Pycnidia always numerous and conspicuous, sessile or shortly stalked, whitish (concolorous with the apothecia), 100–300 μm tall (including stalk) and 60–120 μm diam; stalks (pycnidiophores) simple but occasionally clustered and appearing as if branched at the base; stalk tissue composed of interwoven hyphae *c.* 1–1·5 μm wide that ± separate in K. *Conidiogenous cells* ± cylindrical, 5–10×1–1·5 μm. *Conidia* (*mesoconidia*) cylindrical, eguttulate, 3·8–6×1–1·2(–1·5) μm.

Chemistry: Apothecia, pycnidia and thallus (in section) K−, C+ red, PD−; t.l.c.: gyrophoric acid.

Observations: Micarea pycnidiophora is characterized by its whitish apothecia and concolorous, ± stalked pycnidia, shortly acicular spores, and C+ red reactions (gyrophoric acid). It most closely resembles *M. stipitata*, which differs in having more elongate and often distinctly branched pycnidiophores, larger conidia, and C− reactions (gyrophoric acid absent). *M. globulosella* and *M. synotheoides* have similar acicular spores, but their apothecia are dark-coloured with an olivaceous (K+ violet) pigment, and their pycnidia are inconspicuous and usually immersed in the thallus. Confusion could arise with *Scoliciosporum pruinosum* (P.



Map 21 *Micarea pycnidiophora* ▲ + *Micarea stipitata* ●

James) Vězda and *S. schadeanum* (Erichsen) Vězda, but those species have narrower spores which are spiralled in the ascus and non-micareoid phycobionts (? *Trebouxia*); moreover, *S. pruinosum* has a granular epithecium (granules dissolving in K). Furthermore, these species have inconspicuous (? unknown) pycnidia, and do not contain gyrophoric acid.

For illustrations of conidia and conidiogenous cells, and for further discussions, see Coppins & James (1979).

Habitat and distribution: M. pycnidiophora is a species of old woodlands, in damp, sheltered, and rather shaded situations. It is generally found on areas of ± smooth-bark on the boles of old trees, especially *Fagus* and *Ilex,* but also *Alnus, Quercus,* and *Rhododendron.* Although characteristic of acid bark it has not yet been recorded on conifers.

Its known centre of distribution is the New Forest of Hampshire in southern England, where it is locally frequent. Its other British localities are Sheffield Park in Sussex (on *Rhododendron* with *Gyalideopsis anastomosans*) and the Limb Valley, Yorkshire (its most northerly locality; at base of *Fraxinus*). The latter site is an ancient oak-wood just outside the large industrial city of Sheffield, but *M. pycnidiophora* occurs in an extremely sheltered situation, where it presumably avoids the effects of the high levels of air pollution prevalent in that area. *M. pycnidiophora* is little known outside of Britain, but is reported from Bretagne, France (Coppins, 1971, as '*Bacidia* sp. 2') and the Canary Islands.

36. **Micarea rhabdogena** (Norman) Hedl.
(Fig. 29A)

in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 75, 85 (1892). – *Biatora (Lecidea) rhabdogena* Norman in *Öfvers. K. VetenskAkad. Förh.* **27**: 803 (1870). – *Lecidea rhabdogena* (Norman) Th. Fr., *Lich. Scand.* **2**: 473 (1874). Type: Norway, Nordland, Maalselven, Skjeggenaes, *J. M. Norman* (O – lectotype!; isolectotypes: BM!, O!, S!).

Lecidea glomerella f. ecrustacea Nyl. ex Vainio in *Acta Soc. Fauna Fl. fenn.* **57** (2): 457 (1934). – *Lecidea glomerella* f. *ecrustacea* Nyl. in Elfving in *Medd. Soc. Fauna Fl. fenn.* **2**: 168 (1878); *nom. nudum* (Art. 32). Type: USSR, Karelskaya ASSR, Karelia olonetsensis, Gorki near Svir, *F. Elfving* (H-NYL 19120 – holotype!).

Thallus inapparent, endoxylic; hyphal walls often olivaceous, K+ violet. *Phycobiont* probably micareoid, cells *c.* 5–7 μm diam.

Apothecia numerous, immarginate, convex-hemispherical or tuberculate, black, matt, 0·1–0·3 mm diam, or up to 0·4 mm diam when tuberculate. *Hymenium* 23–30 μm tall; upper part (epithecium) fuscous-brown, HNO_3−, K− but pigment dissolving and fading into solution; remaining (lower) part dilute yellowish brown; hymenium sometimes tinged violet in K (evident after brown pigment has dissolved). *Asci* clavate, 19–28×7–9 μm. *Spores* oblong-ellipsoid, ovoid-oblong or bacilliform, simple or rarely a few 1-septate, 6–9×1·5–2·3 μm. *Paraphyses* numerous, hyaline throughout, *c.* 1 μm wide in mid-hymenium but often widening above to 1·5 μm; sparingly branched and sometimes anastomosing, but becoming richly branched above where their entangled apices, together with the brown pigment, form a ± well delimited epithecium. *Hypothecium c.* 70–160 μm tall, pale, dilute yellowish brown, K−, HNO_3−. *Excipulum* reflexed, dilute to dark fuscous-brown, K− but partly dissolving into solution; hyphae radiating, branched and anastomosing, *c.* 0·7–0·1 μm wide, sometimes widening to 1·5 μm towards the outer edge.

Pycnidia of two types: (a) partly immersed to ± sessile, black, matt, 40–80 μm diam; wall olivaceous, K+ violet; *conidia* (*mesoconidia*) oblong-ellipsoid, oblong-ovate or obovate, *c.* 3·5–4·7×1·4–1·8 μm; (b) immersed between surface wood fibres, black, *c.* 4 μm diam; wall olivaceous, K+ violet; *conidia* (*microconidia*) narrowly cylindrical, 4–4·5×0·7–0·9 μm.

Chemistry: Sections of apothecia C−; material insufficient for analysis by t.l.c.

Observations: M. rhabdogena resembles *M. elachista* in apothecial pigmentation and anatomy, but differs in its endoxylic thallus, smaller and mostly simple spores, and smaller, matt black pycnidia. *M. rhabdogena* is similar in appearance and spore characteristics to *M. misella,* but the latter has an olivaceous, K+ violet hymenium (fuscous pigment lacking) and its mesoconidia are borne in stalked pycnidia. Diminutive, endoxylic forms of *M. denigrata* can be distinguished by the absence of a distinct (fuscous) epithecium, hymenium reacting K+ violet, C+ violet (due to olivaceous pigment) and, usually, C+ orange-red (gyrophoric acid). The mesoconidial states of *M. denigrata* and *M. rhabdogena* are very similar, but *M. denigrata* has longer (4·5–7·5 μm) microconidia, and sometimes has curved macroconidia; macroconidia are apparently not produced by *M. rhabdogena* or the related *M. elachista*.

Habitat and distribution: M. rhabdogena appears to be a rare or much overlooked, exclusively lignicolous species, known so far only from north Norway, mid-Sweden and Karelia. All collections are on rather hard conifer lignum, and associated species include *Calicium trabinellum, Cetraria pinastri, Mycocalicium subtile, Parmeliopsis ambigua, P. hyperopta, Xylographa abietina,* and *X. vitiligo*.

Exsiccata: Malme *Lich. Suec.* 20 (M, S).

37. **Micarea stipitata** Coppins & P. James
(Fig. 29B; Map 21)

in *Lichenologist* **11**: 156 (1979). Type: Scotland, Argyll, Loch Creran, Glasdrum National Nature Reserve, on *Betula*, 27 v 1976, *L. Tibell & Coppins* 2357 (E – holotype!; isotypes: BM!, H!, UPS, hb Poelt!, hb Vězda!).

Thallus and apothecia: more or less identical in appearance and internal anatomy to those of *M. pycnidiophora* (*q.v.*).

Pycnidia always present numerous and conspicuous, borne on distinct whitish stalks (pycnidiophores) which may be simple, bifurcate or to 5-branched, mainly 400–800 μm tall and 60–100(–150) μm diam, often with small irregular clusters of ± superficially encapsulated algae (small granular-areolae). Stalk tissue composed of interwoven hyphae, *c.* 1–1·5 μm wide, which ± separate in K. Pycnidia innate in the apex or apices of pycnidiophores, ± globose or doliiform, *c.* 60–90 μm diam. *Conidiogenous cells* ± cylindrical, 7–11×1·4–2 μm. *Conidia* (*mesoconidia*) cylindrical or narrowly ellipsoid, eguttulate, 6–8×1–1·8 μm.

Chemistry: All parts K−, C−, KC−, PD−; no substances detected by t.l.c.

Observations: See under the related species *M. pycnidiophora* for the differences between them and for comparisons with other similar species.

Habitat and distribution: M. stipitata is characteristic of acid, often leached, bark (or overgrowing bryophytes thereon) on trees in undisturbed woodlands in areas with a high rainfall. It occurs in communities referable (or closely akin) to the *Parmelietum laevigatae* on the trunks of *Betula, Quercus*, and, less frequently, *Alnus, Pinus, Abies,* and *Pseudotsuga*. It has once been found on mossy rocks.

The British distribution of *M. stipitata* is a distinctly more northern and western, as well as more oceanic, than that of *M. pycnidiophora* (see Map 21). It has not yet been found in south-west England but presumably occurs there. Although known from the Azores and the Canary Islands it has not been found elsewhere in Europe, but should be looked for in the hyperoceanic woodlands of, for example, south-west Norway and France (Bretagne).

Additional information: for additional illustrations and some further discussion see Coppins & James (1979).

38. **Micarea subleprosula** (Vězda) Vězda
(Figs 30, 53–54; Map 25)

in Vězda & V. Wirth in *Folia geobot. phytotax, Praha* **11**: 101 (1976). – *Bacidia subleprosula* Vězda in *Preslia* **33**: 366 (1961). Type: Czechoslovakia, Bohemia, Sudety, Krkonoše, Mumlava valley near Harrachov, 900 m, over decaying mosses on granitic rocks, 1960, *A. Vězda* (E – isotype! [t.l.c.: alectorialic acid]).

Thallus: As for *M. leprosula* (*q.v.*) but with a different chemistry (see below).

Apothecia sometimes (? often) absent, immarginate, ± globose and constricted at the base, sometimes irregularly aggregated or tuberculate, grey-brown, brownish black, or black and often with bluish tinge, 0·2–0·8 mm diam. *Hymenium c.* 65–90 µm tall, ± hyaline but upper part olivaceous or dilute reddish brown, K−, HNO_3+ reddish. *Asci* clavate, *c.* 60–70×19–22 µm. *Spores* fusiform, often slightly curved, 3–7(–9)-septate, (35–)40–50(–60) µm. *Paraphyses* numerous, branched and often anastomosing, 1–1·5 µm wide; apices often more richly branched, not or only slightly incrassate (to 1·8 µm). *Hypothecium c.* 120–200 µm tall, ± hyaline or dull straw, but often mottled dilute fuscous-brown (K−) in the upper part; hyphae interwoven, but becoming outwardly orientated towards the hymenium and excipulum, *c.* 0·8–1·5 µm; ascogenous hyphae with swollen cells, *c.* 2–6 µm wide. *Excipulum* distinct in young apothecia, but reflexed and obscured in old apothecia, hyaline or dilute fuscous-brown in part; hyphae radiating, branched and anastomosing, *c.* 1–1·5 µm wide.

Pycnidia not found.

Chemistry: Thallus K−, C+ red, PD+ yellow; sections of apothecia C−; t.l.c.: alectorialic acid plus two unidentified accessory substances.

Observations: Micarea subleprosula is closely allied to *M. leprosula* and sterile thalli of the two species can only be distinguished by their reactions with PD, or by t.l.c. See under *M. leprosula* for further discussion.

For additional illustrations of *M. subleprosula* see Vězda (1961).

Habitat and distribution: M. subleprosula grows over mosses on rocks in much the same habitats in which *M. leprosula* is mostly commonly found. It was originally described from the Sudety mountains of Czechoslovakia, where it occurred at an altitude of 900 m, and I have seen only two additional specimens: from Sweden (Värmland) at 200 m; and Wales (Snowdonia) at *c.* 760 m. It may have been overlooked for *M. leprosula*. However, I have tested numerous individual thalli personally gathered in the field (mainly in Scotland) during the last six years, and all of these were Pd+ red and referable to *M. leprosula*.

39. **Micarea subnigrata** (Nyl.) Coppins & Kilias
(Figs. 31A, 50: Map 22)

in Kilias in *Herzogia* **5**: 391 (1980). – *Lecidea subnigrata* Nyl. in *Flora, Jena* **49**: 370 (1866). – *Lecidea denigrata** [subsp.] *subnigrata* (Nyl.) Crombie, *Lich. Brit.*: 70 (1870). – *Catillaria subnigrata* (Nyl.) Herre in *Proc. Wash. Acad. Sci.* **12**: 94 (1910). Type: Wales, Merioneth, Cader Idris, 1866, *W. A. Leighton* (H-NYL 19136 – lectotype!, sel. Kilias (*loc. cit.*); BM ex K – isolectotype!).

Lecidea confusula Nyl. in *Flora, Jena* **55**: 360 (1872). – *Micarea confusula* (Nyl.) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 76, 86 (1892). Type: Scotland, East Perthshire, Blair Atholl, Craig Tulloch, on mica-schist, 1871, *Crombie* (H-NYL 20191 – lectotype!; BM – isolectotype!).

Thallus effuse, widespreading or as small patches amongst other lichens, of scattered to confluent or clustered, irregularly convex to subglobose areolae. Areolae 0·08–0·45 mm diam (usually at their largest when adjoining apothecia), dark grey-brown, matt or slightly glossy; in section with a hyaline amorphous covering layer *c.* 3–10 µm thick, and outermost hyphae often pale brown (K−); a white medulla often developed in large areolae. *Phycobiont* micareoid, cells *c.* 4–7 µm diam.

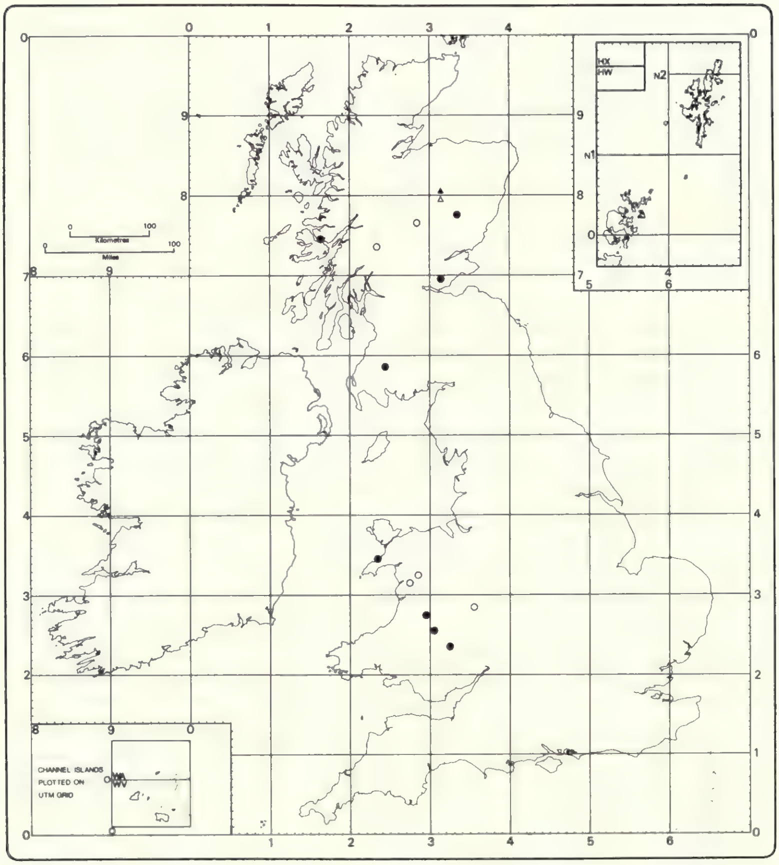
Apothecia usually numerous, scattered to crowded and confluent, immarginate, at first adnate and slightly convex, soon becoming convex-hemispherical and occasionally tuberculate, dark brown (reddish brown when wet) to brownish black, matt or slightly glossy (especially when young), 0·2–0·6 mm diam, or up to *c.* 1 mm diam when tuberculate. *Hymenium* 35–38 µm tall, hyaline but upper *c.* 10–12 µm (epithecium) fuscous brown, K−, HNO_3−. *Asci* clavate 33–35×10–14 µm. *Spores* ellipsoid (0–)1-septate, 8–12×4–5 µm. *Paraphyses* numerous, branched and anastomosing, (1–)1·3–1·7 µm wide, sometimes, gradually widening to 2·5 µm towards apices; hyaline throughout (epithecial pigment confined to gel-matrix). *Hypothecium*

45–160 μm tall, hyaline; hyphae interwoven, some becoming vertically orientated towards the hymenium, *c.* 1·2–1·8 μm wide, intermixed with ± inflated, short-celled ascogenous hyphae *c.* 2·5–5 μm wide. *Excipulum* well developed, 25–45 μm wide, dilute fuscous brown; hyphae radiating, branched and anastomosing, *c.* 1·3–1·7 μm wide.

Pycnidia usually present, immersed within areolae with ostioles visible (×50) as minute pores surrounded by a thin, often slightly raised, dark brown rim; in section with a simple circular or flask-shaped cavity, walls hyaline, or pale brown around the ostiole; of two types: (a) *c.* 80–200 μm diam; *conidiogenous cells* ampulliform to subcylindrical, some with 1–2 percurrent proliferations, 4–10×1·5–2·5 μm, sometimes with swollen base to 4 μm wide; *conida (macroconidia)* helicoid with 2–3 spirals, often appearing 3–5-septate, overall size 7–10×5–6 μm, filaments 1·8–2 μm wide (b) *c.* 40–100 μm diam; *conidiogenous cells* ± cylindrical or ampulliform, 4–10×1–1·4 μm, sometimes with swollen base to 3 μm wide; *conidia* (*microconidia*) cylindrical, 4·6–6×0·8–1 μm.

Chemistry: Thallus K−, C−, PD−; sections of apothecia C−; t.l.c.: no substances.

Observations: Micarea subnigrata is characterized by its dark grey-brown, verrucose-areolate thallus, dark brown apothecia, fuscous brown epithecium and excipulum, colourless hypothecium, and 0–1-septate, ellipsoid spores. However, its most outstanding and characteristic feature is the helicoid shape of its macroconidia (Fig. 50A); such conidia are unique in the genus and apparently so in all pycnidial fungi, whether lichenized or not. In general appearance, habitat and shape and septation of spores *M. subnigrata* could be confused with *M. intrusa*, but



Map 22 *Micarea intrusa* ▲ 1950 onwards △ Before 1950 + *Micarea subnigrata* ● 1950 onwards ○ Before 1950

that species has a green epithecium and a large-celled, non-micareoid phycobiont. The little known *M. curvata* may be closely related to *M. subnigrata*, but can be distinguished by the fabiform or strongly curved spores and C+ red reaction of apothecial sections. With its external and internal fuscous brown colourations *M. subnigrata* could be mistaken for a *Fuscidea*, but species of that genus have broader (*c.* 1·7–2·7 μm) mostly unbranched paraphyses (the apical cell of each being clavate or capitate and often provided with a dark brown 'apical cap'), asci with a thick, strongly amyloid apical wall, and probably referable to the *Teloschistes*-type (Honegger, 1978), and a protococcoid phycobiont, with thick-walled cells, *c.* 10–14 μm diam.

For additional illustrations of *M. subnigrata* see Kilias (1981: 391, 445).

Habitat and distribution: M. subnigrata is confined to hard siliceous rocks in rather exposed situations. The communities in which it occurs are attributable to the *Lecideion tumidae* alliance, especially the *Lecideetum lithophilae* association. The collection (*Coppins* 8417) from Glentrool in Kirkcudbrightshire was made from the south-facing side of a doleritic boulder on a south-facing slope, at an altitude of 135 m; association species were: *Cladonia subcervicornis, Huilia albocaerulescens, H. tuberculosa, Lecanora badia, Lecidea pycnocarpa, Lepraria neglecta, Rhizocarpon obscuratum, R. oederi, Stereocaulon vesuvianum, Trapelia involuta, T.* aff. *obtegens,* and *Andraea* sp. From other British collections the following can be added: *Candelariella vitellina, Catillaria chalybeia, Lecanora intricata, L. polytropa, Lecidea fuliginosa, L. lactea, Lecidella scabra,* and *Parmelia verruculifera.* For information on associated species in its Norwegian locality see *M. intrusa* (Table 5).

M. subnigrata is known from scattered localities in upland districts in the Scottish highlands, Galloway, and Wales; recent field studies indicate that it may be far more common in these and similar areas (e.g. Lake District and Dartmoor) than present records (Map 22) suggest. Outside Britain it is known only from coastal Norway (Hordaland) and south-west Sweden (Halland).

40. **Micarea subviolascens** (Magnusson) Coppins, **comb. nov.** (Fig. 31B)

Lecidea subviolascens Magnusson in *Blyttia* **7**: 30 (1949). Type: Norway, Hordaland, Granvin, Steinsaethorgen, on easily weathered schist in an open windy place of a small hill, 780 m, ix 1944, *J. J. Havaas, Lich. Exs. Norv.* 694 (BG – lectotype!). Topotype material collected in 1949 distributed in Havaas, *Lich. Exs. Norv.* 710 (BG!) and *Lich. Norv. Occid.* 269 (BG!).

Lecidea assimilata f. *aberrans* Th. Fr., *Lich. Scand.* **2**: 523 (1874). Type: Norway, Troms, Tromsø, Fløjfjellet, 1868, *Th. M. Fries* (UPS – holotype!).

Lecidea assimilata var. *hardangeriana* Vainio in *Acta Soc. Fauna. Fl. fenn.* **57** (2): 374 (1934). – *Lecidea assimilata* var. *hardangeriana* Vainio *in* Havaas in *Bergens Mus. Årb.* **1909** (1): 29 (1909); *nom. nudum* (Art. 32). Type: Norway, Hordaland, Granvin, Smøreggen, 650 m, 22 viii 1902, *J. J. Havaas, Lich. Exs. Norv.* 139 (BG – lectotype! [t.l.c.: no substances]; isolectotypes: BG!, H!).

Thallus effuse, saxicolous, composed of ± confluent, white to pale brown, convex, verrucose-areolae *c.* 0·1–0·5(–0·8) mm diam; with age the crust may thicken (to *c.* 1 mm) and become cracked and divided into 'islands' *c.* 1–2 μm wide. Areolae in section, sometimes with a hyaline amorphous covering layer *c.* 5–7 μm thick, upper *c.* 20 μm of areolae often tinged dilute olivaceous and Kf+ violet (pigment confined to the weak gel-matrix). Thallus hyphae 1·7–2·5 (–3) μm wide. *Phycobiont* micareoid, cells 4–7 μm diam. *Cephalodia* (?): spaces between areolae often filled by black, loose clusters of *Stigonema*.

Apothecia numerous, immarginate, adnate, convex to subglobose, black, matt, 0·3–0·6(–0·8) mm diam, often confluent, or forming tuberculate clusters up to 1·2 μm diam. *Hymenium* 40–55 μm tall, dark green (K+ violet, HNO_3+ purple-red) above, and below in vertical streaks, otherwise dilute greenish or ± hyaline. *Asci* clavate, 38–48×10–15 μm. *Spores* ellipsoid, ovoid-ellipsoid or oblong-ellipsoid, simple, 9–16(–17)×4–5 μm. *Paraphyses* numerous, simple below, but in upper part often forked or with short lateral branches, 1–1·8(–2) μm wide, sometimes widening above to 3 μm; apical walls hyaline although surrounded by densely pigmented gel-matrix. *Hypothecium* 150–300 μm tall, dark purple-brown, K+ purple intensifying, or upperpart K+ dark green; all parts HNO_3+ purple-red; hyphae interwoven, but ±

vertically arranged in upper part, 1·5–2·5 μm wide, embedded in densely pigmented gel-matrix; ascogenous hyphae *c.* 2·5–5 μm wide. *Excipulum* ± distinct in young apothecia, but soon reflexed, dark purple-brown (K+ dark green) within, changing to green (K+ green intensifying) towards the outer edge; hyphae radiating, branched, *c.* 1·5–2 μm wide.

Pycnidia: Not found.

Chemistry: Thallus K−, C−, KC−, PD−; t.l.c.: no substances.

Observations: In his protologue, Magnusson allied his new species with the *Lecidea [Micarea] sylvicola* group. However, Th. M. Fries, 75 years earlier, was probably nearer the truth when he described material of *M. subviolascens* as a form ('*aberrans*') of *Lecidea [Micarea] assimilata*. In my opinion *M. subviolascens* is very closely related to *M. assimilata*, and the reader is referred to the account of that species for further discussions.

Habitat and distribution: M. subviolascens appears to have a very restricted distribution, being known only from the provinces of Troms and Hordaland in Norway. It is the only known saxicolous member of the *M. assimilata* group, and occurs on acidic rocks (schists and gneiss) in rather open situations. In the Hordaland localities it was collected at altitudes of 650 m and 795 m. The labels accompanying the specimens provide little extra ecological information, and the specimens have few associated species, although *Pyrenopsis pulvinata* and *Rhizocarpon obscuratum* have been noted.

Exsiccata: Havaas *Lich. Exs. Norv.* 139 (BG, H), 694 (BG), 710 (BG). Havaas *Lich. Norv. Occid.* 269 (BG).

41. **Micarea sylvicola** (Flotow) Vězda & V. Wirth
(Figs 31C, 51A; Map 23)

in *Folia geobot. phytotax, Praha* **11**: 99 (1976). – *Lecidea sylvicola* Flotow, *Lich. Schles.* 171 (1829). Type: Poland, Schlesien, *Flotow, Lich. Exs.* 171A (UPS – lectotype!, sel. Hertel (1975: 74); WRSL – isolectotype!).

Lecidea aggerata Mudd, *Man. Br. Lich.*: 208 (1861). Type: England, Yorkshire, Battersby, *Mudd, Lich. Brit.* 175 (BM – lectotype!; isolectotypes: E!, H-NYL 14016!, M!, MANCH!).

Lecidea incincta Nyl., *Lich. Scand.*: 231 (1861). Type: Finland, Satakunta, Källfjärd [Ahlainen: Kellahti], 1859, *A. J. Malmgren* (H – holotype!).

Biatora smaragdina Arnold in *Verh. zool. bot. Ges. Wien* **19**: 613 (1869). Type: Italy, Trentino-Alto Adige, 'Melaphyr in Walde unterhalb Bad Razzes am Schlern [Monte Pez]', vii 1867, *Arnold* (M – holotype!).

Lecidea hellbomii Lahm in *Flora, Jena* **53**: 177 (1870). Type: Sweden, Närke, Vredstorp, Urby, on granitic rock, 1869, *P. J. Hellbom* (M – lectotype!).

Lecidea sylvicola f. *sublivida* Vainio in *Medd. Soc. Fauna Fl. fenn.* **10**: 104 (1883). – *Lecidea sylvicola* var. *sublivida* (Vainio) Vainio in *Acta Soc. Fauna Fl. fenn.* **57** (2): 298 (1934). Type: Finland, Ostrobottnia kajanensis, Kuhmo,Kylmälä, 1877, *E. A. Vainio* (TUR-VAINIO 25226 – holotype!).

Lecidea hypocyanea Vainio in *Acta Soc. Fauna Fl.fenn.* **57** (2): 300 (1934), non Stirton (1879). – *Lecidea vainioi* Magnusson in *Blyttia* **7**: 31 (1949); *nom. nov.* Type: Finland, Regio aboënsis, Turku, Hirvensalo, 10 vii 1924, *E. A. Vainio* (TUR-VAINIO 33172 – lectotype!, sel. Hertel (1975: 74)).

Lecidea sylvicola var. *flotowii* Vainio in *Acta Soc. Fauna Fl. fenn.* **57** (2): 297 (1934); *nom. inval.* (Art. 26).

Thallus effuse, thin and ± smooth or weakly rimose to rather thick, uneven and coarsely rimose, or sometimes with irregularly granular or verrucose areolae up to 0·3 mm diam, pale buff, pale to dark grey or bluish grey; in section without a cortex or hyaline covering layer, but walls of outermost hyphae sometimes greenish, K−, HNO_3+ purple-red. *Phycobiont* not micareoid; cells thin-walled, ± globose and *c.* 5–12 μm diam, or ellipsoid and up to 15×10 μm.

Apothecia numerous, convex-hemispherical from the start, often becoming ± globose or tuberculate, black and often with bluish tinge, sometimes dark blue-grey (deep shade forms), 0·2–0·5 diam, or to 1·2 mm when tuberculate. *Hymenium* 40–60(–70) μm tall, dilute bright or sordid aeruginose, but often darkish aeruginose in upper and lower parts, and in vertical streaks (due to presence of stout pigmented paraphyses), K− or + aeruginose intensifying, HNO_3+ purple-red. *Asci* cylindrical-clavate, *c.* 35–45×8–12 μm. *Spores* ellipsoid or ovoid, simple (an occasional 1-septate spore seen in a few collections), (6–)7–10×(2·5–)3–4·5 μm. *Paraphyses* rather scanty, of two types: *p.p.* evenly distributed, irregularly flexuose, simple or sparingly branched, often anastomosing, hyaline, thin, 0·7–1 μm wide, sometimes widening above to 1·8 μm; *p.p.* fewer in number, as scattered individuals or in small fascicles, straight, simple or occasionally forked above, stout, coated ± throughout (but most intensely so around the apices) by dark green pigment and appearing *c.* 2–3 μm wide, apices sometimes incrassate and up to 4 μm wide. *Hypothecium* 90–200 μm tall, dark aeruginose or olive-black, K− or + green intensifying; lower ('core') part, or rarely the entire hypothecium, dark purplish brown, K+ purple intensifying; all pigments HNO_3+ purple-red; hyphae coated with dense dark green pigment and 2–3 μm wide (overall), interwoven but becoming vertically orientated towards the hymenium and some continuing into it as stout, pigmented paraphyses; ascogenous hyphae similarly pigmented, with swollen cells *c.* 3–5 μm wide. *Excipulum* not evident, even in sections of young apothecia.

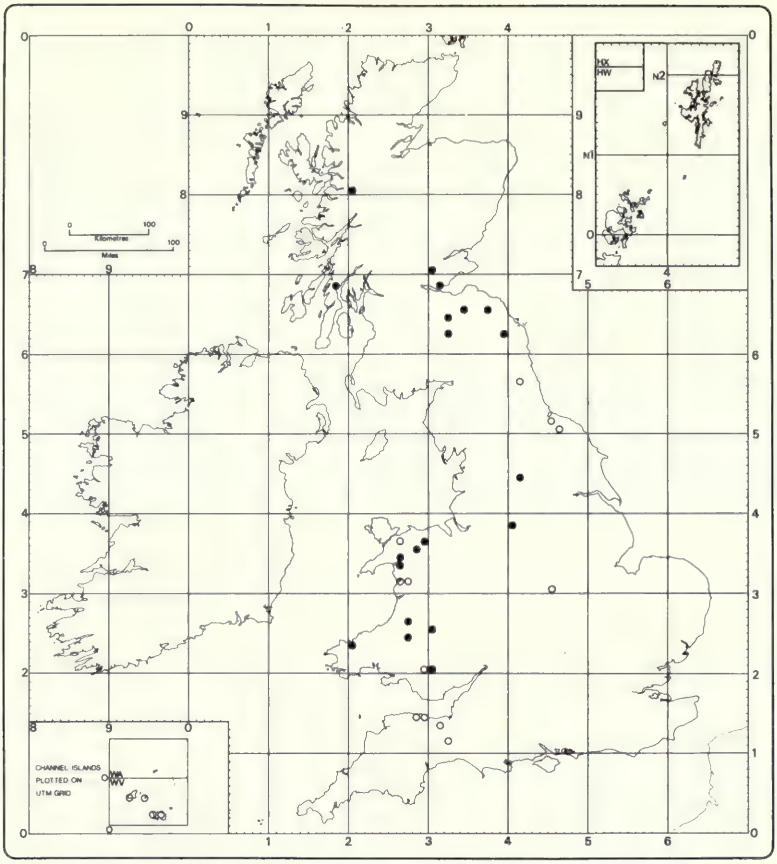
Pycnidia usually present and numerous, immersed, black, 40–200 μm diam; in section with a single circular or ovate locule but often becoming internally convoluted with up to 6 locules, wall dark green K−, HNO_3+ purple-red in upper part, turning paler below and dilute brownish or ± hyaline at the base; *conidiogenous cells* irregularly subcylindrical, 5–10×1·2–1·5 μm, often with one or two percurrent proliferations; *conidia* (*mesoconidia*) ± cylindrical or sometimes oblong-obovoid, sometimes biguttulate and often ± constricted in the middle, 3·8–6(–6·6)×1–1·7(–2) μm.

Chemistry: Thallus K−, C−, KC−, PD−; sections of apothecia C−; t.l.c.: no substances.

Observations: Micarea sylvicola is characterized by its convex-globose, often tuberculate, black apothecia, green or blue-green hymenium, very dark green-black or brown-black hypothecium (appearing green, or rarely purplish, in K), and ellipsoid to ovoid, simple spores. The variation in hypothecial pigmentation is similar to that found in such species as *M. assimilata, M. crassipes,* and *M. melaena. M. tuberculata* is rather similar to *M. sylvicola* but has generally smaller apothecia, a more shallow hymenium, narrower, oblong-ovoid spores that are often 1-septate, and shorter conidia. Forms of *M. bauschiana* with greenish pigment in the hypothecium have been confused with *M. sylvicola*, however the pigment is always dilute and confined to the gel-matrix such that the hyphae appear hyaline in K (at ×1000). The thallus of *M. sylvicola* is often provided with a blue-grey tinge due to green-pigmented hyphae near the surface; such coloration has not been noticed with the thalli of *M. bauschiana* and *M. tuberculata*. Another species often confused with *M. sylvicola* is *Lecidea erratica* Körber, which can be distinguished by its thinly marginate young apothecia, and distinct excipulum when observed in section.

Habitat and distribution: M. sylvicola is mainly found on dry shaded rocks in the communities belonging to *Micareetum sylvicolae*, but it sometimes occurs in periodically wetter situations on rock faces, upper sides of boulders, and loose stones in woodlands where it may be associated with such species as *Baeomyces rufus, Cystocoleus ebeneus, Fuscidea recensa, Huilia tuberculosa, Parmelia saxatilis, Rhizocarpon hochstetteri, R. obscuratum, R. oederi, Scoliciosporum umbrinum, Trapelia involuta*, and in one instance (Coed Hafod, Denbigh) *Bacidia vezdae.* In addition, it is sometimes found on old fence posts in upland districts.

In the British Isles *M. sylvicola* is more confined to upland districts and is less common than *M. bauschiana.* It seems to be particularly prevalent in Wales and south-east Scotland, and curiously rare in western Scotland and Ireland. Further field-work is required to establish whether or nor its apparent scarcity in these latter areas is real or merely an artefact resulting from uneven recording. However, my field observations in western Scotland suggest that its niche in the *Micareetum sylvicolae* is there occupied by *M. lutulata. M. sylvicola* is widely distributed in Scandinavia, but rarely found from north of about latitude 67°N. Elsewhere in Europe I have seen specimens from Germany (Hessen and Baden-Württemberg), eastern Austria, northern Italy, south-west Poland and the mountain regions of Czechoslovakia. From outside Europe I can confirm its presence in north-eastern North America (New York and Newfoundland).



Map 23 *Micarea sylvicola* ● 1950 onwards ○ Before 1950

Exsiccata: Arnold *Lich. Exs.* 409A (BM ex K, M, MANCH, WRSL), 409B *p.p.* (BM ex K, M). Flotow *Lich. exs.* 171A (WRSL). Johnson *Lich. Herb.* 434 *p.p.* (BM). Kav. & Hilitzer *Crypt. Cech.* 269 (UPS). Körber *Lich. Sel. Germ.* 75 (M). Larb. *Lich. Caesar. Sarg.* 84 (ABD, BM, MANCH). Larb. *Lich. Herb.* 304, 305 *p.p.* (BM). Malme *Lich. Suec.* 199 (M, S). Mudd *Lich. Brit.* 175 (BM, E, M, MANCH). Norrl. & Nyl. *Herb. Lich. Fenn.* 763 (BM, H, TUR, WIS), 764 (BM, H, WIS). Räsänen *Lich. Fenn.* 672 *p.p.* (M). Suza *Lich. Bohem.* 131 (M). Vězda *Lich. Sel.* 957, 1341 (BM). Zwackh *Lich. Exs.* 535, 596 (M), 597 (UPS), 780 (M), 919 (BM, M).

42. **Micarea synotheoides** (Nyl.) Coppins
(Figs. 31D–E, 43D–E; Map 24)

in Topham & Walker in *Lichenologist* **14**: 67 (1982). – *Lecidea synotheoides* Nyl., *Lich. Jap.*: 63 (1890). – *Catillaria synotheoides* (Nyl.) Zahlbr., *Cat. lich. univ.* **4**: 78 (1926). Type: Japan, 'Itjgome' (or 'Itchigômé'), on lignum, 1879, *E. Almquist* (H-NYL 19101 – lectotype!; S – isolectotype!).

Thallus effuse, of scattered to coherent, or clustered, granular areolae. Areolae *c.* 20–70 μm diam, dull grey-green (never whitish) to dark olivaceous or blackish, appearing ± gelatinous when wet, usually ± discrete but often coalescing to form a thin uneven crust; a thin white prothallus sometimes visible between scattered areolae. Areolae in section without an amorphous covering layer; outer hyphae often with olivaceous or brownish, K+ violet walls. *Phycobiont* micareoid, cells *c.* 4–7 μm.

Apothecia immarginate, convex-hemispherical to ± globose, often tuberculate, grey-black or brown-black, matt, sometimes grey (shade forms), 0·1–0·3 mm diam, or up to 0·5 mm diam when tuberculate. *Hymenium* 35–45 μm tall, dilute olivaceous or dilute olive-brown, K+ violet: pigment confined to gel-matrix. *Asci* clavate, 30–40×9·5–12 μm. *Spores* ± acicular or rod-shaped, curved or ± straight, 1–7(–11)-septate, 14–35(–43)×1·8–2·5(–3) μm. *Paraphyses* numerous, branched, sometimes anastomosing, 0·8–1 μm wide, sometimes widening to 1·5 μm towards their apices; apical walls hyaline. *Hypothecium* 60–100 μm tall, hyaline, or dilute olivaceous and then Kf+ violet; hyphae hyaline, 1–2 μm wide, interwoven or some ± vertically orientated in the upper part; intermixed with short-celled ascogenous hyphae, *c.* 2–4 μm wide. *Excipulum* indistinct, evident in sections as a narrow, reflexed, non-amyloid lateral border to the hymenium, hyaline or pale olivaceous (then K+ violet), varying from paler to darker than the hymenium; hyphae hyaline, radiating branched and anastomosing, *c.* 1 μm wide.

Pycnidia frequent but inconspicuous, immersed within areolae, or emergent to sessile, whitish to grey-black; walls dull olivaceous (pigment often more intense around the ostioles), K+ violet. Pycnidia of two types: (a) 60–120 μm diam, immersed, or emergent with gaping ostioles; *conidia* (*mesoconidia*) ± cylindrical to fusiform, 4·5–6×1·2–1·5 μm; (b) 30–40 μm diam, immersed to sessile, but ostioles not gaping; *conidia* (*microconidia*) short-cylindrical, 3·8–4·8×0·8–1 μm.

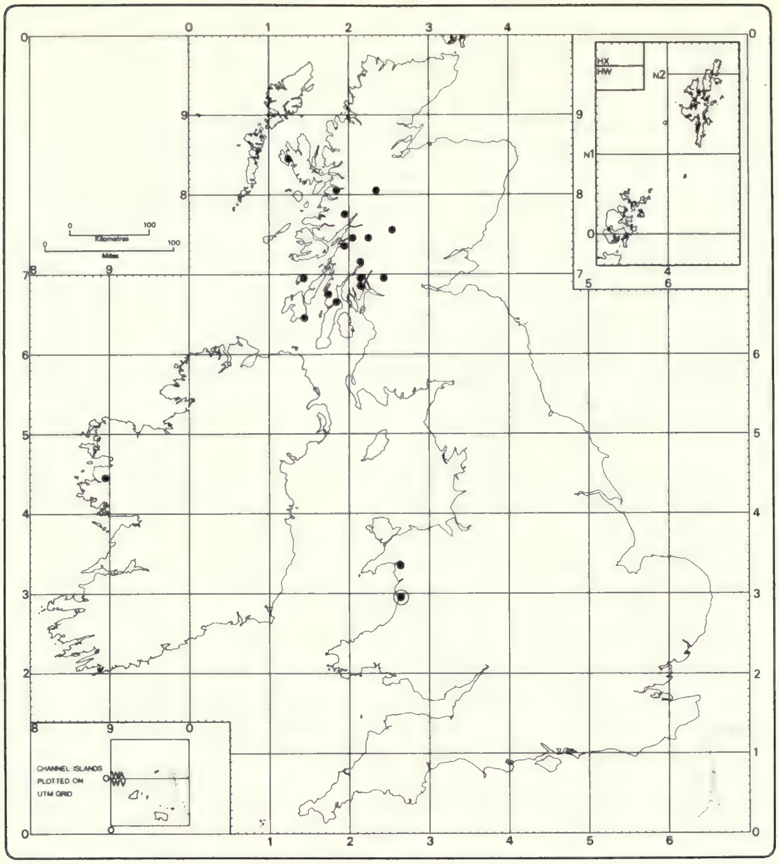
Chemistry: Thallus C−, K−, PD−; sections of thallus and apothecia C− (but olivaceous parts C+ violet due to pigment); t.l.c.: no substances detected.

Observations: Micarea synotheoides is characterized by its ± acicular or rod-shaped spores, K+ violet hymenium, and olivaceous thallus which is ± gelatinous when wet. *M. globulosella* is very similar, but differs in having a thallus of whitish or grey, somewhat larger areolae containing gyrophoric acid. *M. nitschkeana* differs in the same ways, and in addition has shorter (rarely over 17 μm) spores and longer microconidia. *M. globulosella* and *M. synotheoides* have been confused with *Bacidia beckhausii* (see p. 196) which has similar spores, pigmentation and paraphyses, but can be distinguished by its large-celled (*c.* 8–14 μm diam) phycobiont, excipulum of coherent (in K) hyphae, smaller conidia (one type only, *c.* 2·8–3·5×1–1·4 μm), often pruinose apothecia, and usual occurrence on less acidic bark (especially of *Acer, Fraxinus, Populus,* and *Ulmus*), although it does occasionally occur on *Quercus* trunks and more rarely on lignum.

Of the four Japanese specimens, two are on bark and two (type material) are on lignum. They all have rather short spores (14–26 μm), but appear to agree in most other respects with collections from Britain and the Atlantic islands. Unfortunately I was unable to find mesoconidia in the Japanese specimens. For the time being, I consider the Japanese and Atlantic populations as conspecific, especially as the British collections exhibit considerable variation in spore septation and length. Further collections from Japan are required to finally establish the relationship between the two populations.

Habitat and distribution: M. synotheoides is an oceanic species mostly found in wooded valleys on bark or over bryophytes, on the trunks of, for example, *Alnus, Betula, Quercus, Larix, Pinus,* and *Pseudotsuga,* in communities in, or related to, the *Parmelion laevigatae* alliance. British collections include the following associated lichens: *Bryoria fuscescens, Chrysothrix candelaris, Cladonia coniocraea, C. squamosa, Haematomma elatinum, Hypogymnia physodes, Lecanactis abietina, Lecidea icmalea, Micarea alabastrites, M. cinerea, M. peliocarpa, M. stipitata, Mycoblastus sterilis, Ochrolechia androgyna, Parmelia saxatilis, Pertusaria amara, Platismatia glauca, Sphaerophorus globosus, Trapelia corticola in ed.,* and *Usnea subfloridana.* The single British collection on lignum (*Coppins* 2299) was on a rotting trunk of *Pinus.* In the Canary Islands it occurs on *Erica arborea* in a photophobus and hydrophilic community composed of crustose lichens with Atlantic distributions (Topham & Walker, *loc. cit.*). In the Azores it occurs in a more or less identical community on *Cryptomeria.*

Apart from the type locality in Japan, it is known only from western Britain, the Azores, and the Canary Islands (Tenerife). It should be sought for in suitable habitats in other oceanic parts of Europe (e.g. south-west Norway, Bretagne, the Pyrénées, and Portugal).



Map 24 *Micarea globulosella* ◉ 1950 onwards + *Micarea synotheoides* ● 1950 onwards ○ Before 1950

43. **Micarea ternaria** (Nyl.) Vězda
(Figs 32B, 52; Map 25)

Sched. Lich. Sel. Exsicc. 858 (1970). – *Lecidea sabuletorum* f. *ternaria* Nyl. in *Not. Sällsk Fauna Fl. fenn. Förhandl.* **8**: 151 (1866). – *Lecidea ternaria* (Nyl.) Nyl. in *Flora, Jena* **60**: 232 (1877). Type: USSR, Lapponia murmanica, Kola Peninsula, 'Olenji', 1861, *N. I. Fellman* (H-NYL 18682 – holotype! [t.l.c.: no substances]).

Thallus effuse, muscicolous, composed of scattered to confluent, convex to irregularly subglobose areolae [? or saxicolous and obsolete – see 'observations']. Areolae cream-white to ash-grey, *c.* 80–300 μm diam; in section with hyaline amorphous covering layer *c.* 7–10 μm tall, and outermost hyphae with greenish (K−, HNO_3+ red) walls. *Phycobiont* micareoid, cells *c.* 4–7 μm diam.

Apothecia numerous, black, matt or slightly glossy, 0·15–1 mm diam; at first (below 0·3 mm diam) ± globose or turbinate, later expanding to become broadly convex and ± adnate, sometimes faintly marginate. *Hymenium c.* 60–70 μm tall, merging imperceptibly into the hypothecium; upper *c.* 10–15 μm (epithecium) dark aeruginose-green, K−, HNO_3+ purple-red; remaining (lower) part ± hyaline with dilute green vertical streaks. *Asci* clavate. *Spores* fusiform, sometimes slightly curved, (0–)1–3-septate, 13–22(–24)×3·5–5 μm. *Paraphyses* numerous, sparingly branched below but richly branched in epithecium, often anastomosing, *c.* 1–1·8 μm wide; apices often slightly incrassate and surrounded by dense pigment, and up to 3 μm wide. *Hypothecium* up to 380 μm tall; upper third to half, dilute olivaceous or dilute dull brown; lower part ± hyaline; hyphae hyaline *c.* 0·7–1·5 μm wide, interwoven or becoming vertically or outwardly orientated towards the hymenium and excipulum; hyphae in upper part of hypothecium intermixed with inflated, short-celled ascogenous hyphae. *Excipulum* usually distinct, hyaline, or tinged aeruginose or olive-green in parts; hyphae radiating, branched and anastomosing, 0·7–1·7 μm wide.

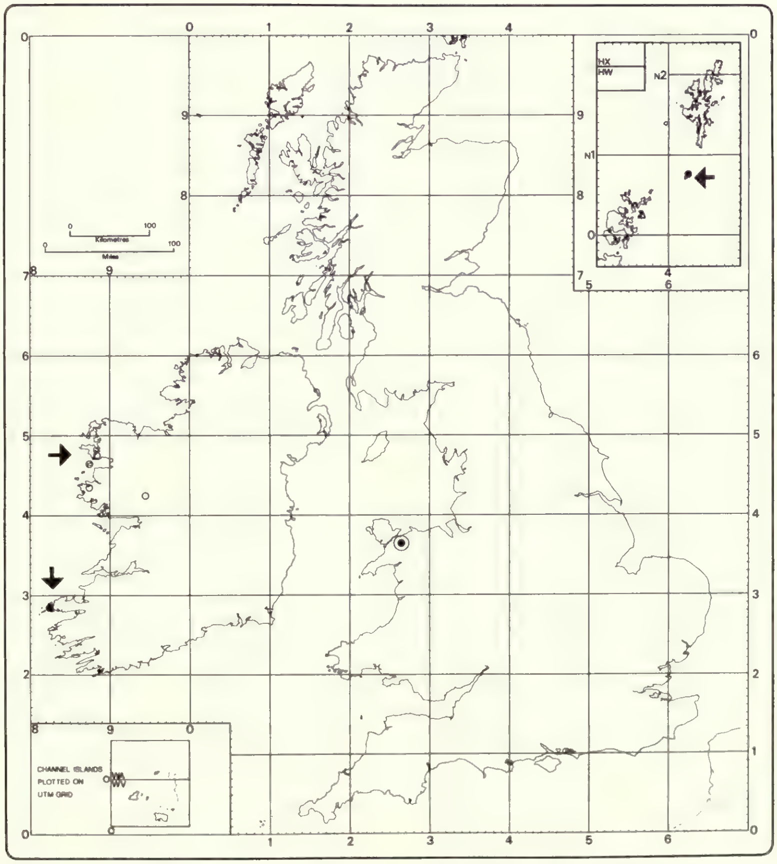
Pycnidia rather numerous, sessile, black, 100–140(–200) μm diam, ostioles often gaping; walls dark olive-green (K−, HNO_3+ red) above and at the sides, but becoming hyaline towards the base. *Conidia* (*mesoconidia*) cylindrical or oblong-ellipsoid, sometimes faintly biguttulate and slightly constricted in the middle, 4·6–6·3×1·2–1·7 μm. Macro- or microconidial states not found.

Chemistry: Thallus K−, C−, PD−; sections of apothecia C−; t.l.c.: no substances.

Note: The above description is based largely on Alaskan specimens (*Thomson* 9188).

Observations: M. ternaria is very close to *M. lignaria* but differs in having shorter spores that are never more than 3-septate, and in completely lacking lichen substances. In addition its apothecia have a more flattened appearance (sometimes with a faint marginal rim), and a ± clearly defined excipulum when viewed in vertical section. It is superficially similar to dark forms of *M. peliocarpa* but that species contains gyrophoric acid (thallus and apothecia in section C+ orange-red), has a hyaline hypothecium, and is not known to have pycnidia which contain mesoconidia.

Having found most herbarium specimens named '*ternaria*' to belong to *M. lignaria* or *M. peliocarpa* I suspected the name to be a synonym of one of these two species. The holotype of



Map 25 *Micarea subleprosula* ◉ 1950 onwards + *Micarea* cf. *ternaria* ● 1950 onwards ○ Before 1950

Lecidea milliaria f. *ternaria* is very fragmentary and my first impression was that it was a diminutive specimen of *M. lignaria,* even though I failed to obtain a positive reaction with PD. This opinion was changed by my subsequent examination of the Alaskan material which is identical to the holotype in all respects but larger and in better condition.

Several problematical collections from the British Isles (Shetland Islands and western Ireland) are provisionally referred to *M. ternaria*. They were all collected in coastal districts on hard siliceous rocks and have a ± obsolete thallus (PD− in microscopical preparations), rather flattened apothecia, and 0–3-septate spores. The specimen from Fair Isle has pycnidia, containing mesoconidia 5·2–6·8×1·2–1·8 μm (Fig. 52C). The discovery of an arctic species, such as *M. ternaria*, in coastal Britain is not without precedent. Examples are *Lecanora straminea* found in the Shetland Islands, Flannan Islands, and St Kilda, and *Bacidia subfuscula* found on North Rona, the Farne Islands, and as far south as the north coast of Norfolk and the Scilly Isles. A better understanding of the variability in habit and habitat of *M. ternaria* in the arctic should help to clarify the taxonomic relationships between the arctic and British populations. In addition, relevant material should be sought in coastal Norway.

Habitat and distribution: On mosses and plant debris on the ground in coastal regions of arctic Europe and North America (northern Alaska). The Alaskan material (*Thomson* 9188) was growing with *Micarea turfosa* and *Siphula ceratites*. Southern populations on rocks may be represented in the British Isles (see 'observations' above).

44. **Micarea tuberculata** (Sommerf.) R. Anderson
(Figs 32A, 34, 51B; Map 26)

in *Bryologist* **77**: 46 (1974). – *Lecidea tuberculata* Sommerf., *Suppl. Fl. Lapp.*: 160 (1826). Type: Norway, Nordland, Saltdalen, Fiskevaagmöllen, iii 1822, *S. C. Sommerfelt* (O – lectotype!; UPS – isolectotype!).

Lecidea latens Taylor *in* Mackay, *Fl. Hib.* **2**: 259 (1836). Type: Ireland, Wicklow, The Dargle, *T. Taylor* (BM – lectotype!).

Lecidea botryocarpa Nyl. in *Flora, Jena* **48**: 603 (1865). Type: USSR, Karelskaya ASSR, Karelia onegensis, 'ad Onegam, Kapselka, 1863, *T. Simming* (H-NYL 10766 – holotype!).

Lecidea subinfidula Nyl. in *Flora, Jena* **52**: 295 (1869). Type: Finland, Lapponia enontekiensis, Naimakka, 29 viii 1867, *J. P. Norrlin* 656 (H – lectotype!; UPS – isolectotype!).

Lecidea tuberculata var. *scandinavica* Vainio in *Acta Soc. Fauna Fl. fenn.* **57** (2): 309 (1934). Type: Finland, Tavastia australis, Lammi, Evo, Lapinkallio, 1866, *Norrlin* (H-NYL 10767 – lectotype!).

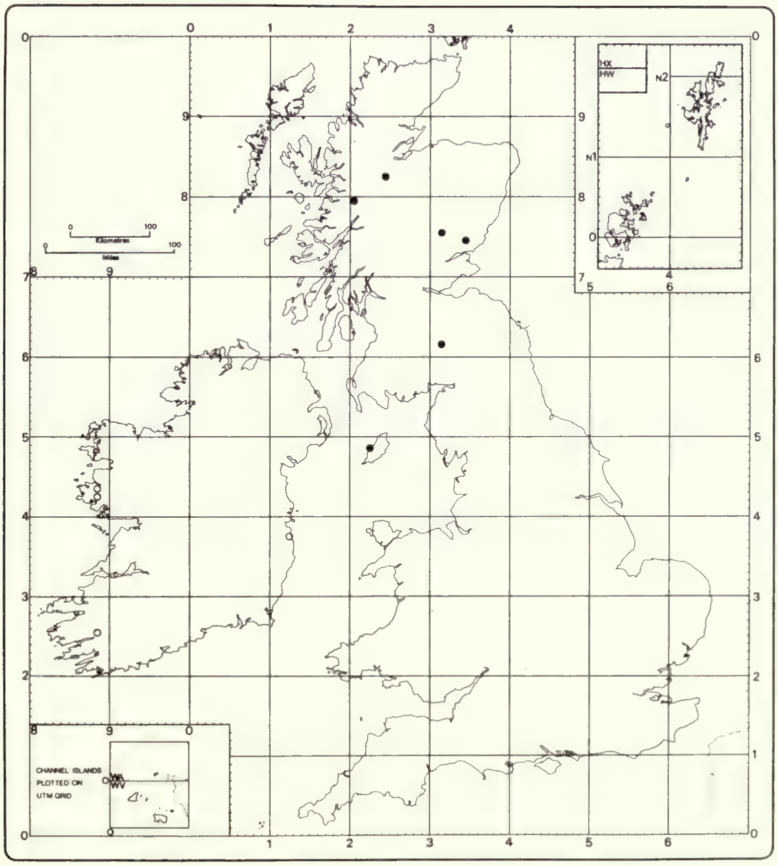
Thallus effuse, minutely scurfy-granular, or sometimes forming an irregularly rimose crust up to 0·2 mm thick, more rarely forming irregularly verrucose areolae *c.* 0·06–0·2(–0·3) mm diam; greenish buff, pale buff or greenish white; thin wefts of white prothalline hyphae sometimes visible. *Phycobiont* not micareoid; cells ± globose, thin-walled, 5–10(–12) μm diam, or irregularly ellipsoid and up to 15×7 μm.

Apothecia numerous, convex-hemispherical and immarginate from the start, often becoming ± globose or tuberculate, black and often with bluish tinge, matt, 0·16–0·3(–0·4) mm diam, or 0·24–0·55 mm diam when tuberculate. *Hymenium* 30–35 μm tall, dilute green or aeruginose, K− or + intensifying, HNO_3+ purple-red, often with darker vertical streaks due to the presence of stout, pigmented paraphyses. *Asci* cylindrical-clavate, 25–30×7–9 μm. *Spores* oblong-ovoid or oblong-ellipsoid, 0–1-septate, 5·5–8(–9)×1·5–2·5 μm. *Paraphyses* rather scanty, of two types (Fig. 34): *p.p.* evenly distributed, irregularly flexuose, simple or sparingly branched, often anastomosing, thin, 1–1·5 μm wide, sometimes widening to 1·7 μm above, walls hyaline throughout and without adhering pigment; *p.p.* fewer in number, as scattered individuals or in small fascicles, straight, simple or occasionally forked above, stout, coated ± throughout by dark greenish pigment and appearing *c.* 2–3 μm wide, apices sometimes ± incrassate and up to 4 μm wide (including pigment). *Hypothecium c.* 80–115 μm tall, aeruginose- or olive-black, K+ aeruginose intensifying; hyphae coated with dense dark green pigment and 2–3 μm wide (overall), interwoven but becoming vertically orientated towards the hymenium and some continuing into it as stout, pigmented paraphyses; ascogenous hyphae similarly pigmented, with swollen cells *c.* 3–5 μm wide. *Excipulum* not evident, even in sections of young apothecia.

Pycnidia often present, ± immersed, black, 60–120 μm diam, ostioles often gaping; walls dark aeruginose, K−, HNO_3+ red; *conidiogenous cells* slender, cylindrical, 5–10×1–1·5 μm, often with a swollen, sometimes pigmented, base up to 3·2 μm wide, and sometimes with one or two percurrent proliferations; *conidia* (*mesoconidia*) ± cylindrical, sometimes faintly biguttulate, 3–4·3×1–1·4 μm.

Chemistry: Thallus K−, C−, KC−, PD−; sections of apothecia C−; t.l.c.: no substances.

Observations: Micarea tuberculata is characterized by its rather small, markedly convex, often tuberculate, blackish apothecia, blue-green hymenium, aeruginose-black hypothecium and small, ovoid-oblong, 0–1-septate spores. The relative proportion of simple to 1-septate spores can vary greatly between collections, and in some specimens no septate spores can be found. *M. tuberculata* has often been confused with forms of *M. sylvicola* with small, immature spores, but such spores are always ellipsoid or ovoid-ellipsoid, and quite distinct from the predominantly oblong-ovoid spores of *M. tuberculata*. If pycnidia are present the two species can be separated on the size of their conidia, which are significantly longer (*c.* 4–6 μm) in *M. sylvicola. M. olivacea* (*q.v.*) is superficially similar to *M. tuberculata*, but has slightly larger spores, shorter conidiogenous cells, and a micareoid phycobiont. Also of similar appearance is *Psilolechia clavulifera* (p. 201), but it has smaller spores, a pale hypothecium, numerous, stout, non-pigmented paraphyses, and a very different phycobiont.



Map 26 *Micarea tuberculata* ● 1950 onwards ○ Before 1950

Habitat and distribution: M. tuberculata is found on rocks, stones, and tree roots, etc. in dry, sheltered underhangs, and is a faithful member of the *Micareetum sylvicolae*. In the British Isles it has scattered localities in the north and west; although not yet known from the mainland in England and Wales it is expected to occur in those areas in suitable terrain (e.g. the Lake District, Dartmoor and Snowdonia). It is undoubtedly much overlooked, but appears to be genuinely rarer than *M. bauschiana* and *M. sylvicola,* with which it often occurs.

It appears to be widely distributed in Fennoscandia where it is known from as far north as Nordland in Norway and Lycksele Lappmark in Sweden. It seems to be rare elsewhere in Europe, but I have seen material from southern Germany, northern Italy, and the Tatra mountains of Czechoslovakia.

Exsiccata: Arnold *Lich. Exs.* 1057 (BM ex K, M). Larb. *Lich. Herb.* 227 *p.p.* (BM). Rabenh. *Lich. Eur.* 648 *p.p.* (BM). Räsänen *Lich. Fenn.* 512 (BM, BM ex K), 672 *p.p.* (BM, LD-mixed with *M. lutulata*, M-mixed with *M. sylvicola*).

45. **Micarea turfosa** (Massal.) Du Rietz
(Fig. 33; Map 27)

in *Svensk bot. Tidskr.* **17**: 94 (1923). – *Biatora turfosa* Massal., *Ric. Lich. Crost.*: 128 (1852). Type: specimen unlocalized but probably from Sudety (Sudeten Mountains) in SW Poland, 'Flotow Lich. exs. 130! hb. Flotow' (VER – holotype!).

Biatora turfosa verrucula* Norman in *K. nor. Vidensk. Selsk. Skr.* **5**: 353 (1868). – *Lecidea verrucula* (Norman) Th. Fr., *Lich. Scand.* **2**: 523 (1874). – *Micarea verrucula* (Norman) Hedl. in *Bih. K. svenska VetenskAkad. Handl.* III, **18** (3): 84, 95 (1892). Type: Norway, Nordland, 'supra Heminghyt convallis Bejeren', *J. M. Norman* (– lectotype!; isolectotypes: LD!, M!, O!).

Thallus effuse but often forming rounded patches about 3–5 cm diam, thin, ± uneven but not forming distinct areolae or goniocyst-like granules, blackish grey or brown-black but shaded portions sometimes dull grey-green, often appearing ± gelatinous when moist. Thallus in section up to 70 μm thick, ecorticate and without an amorphous covering layer; outermost hyphae 2–4 μm wide with walls thickened by dark green pigment, K–, HNO_3+ red; internal hyphae hyaline, *c.* 1–1·5 μm wide. *Phycobiont* micareoid, cells 4–7 μm diam.

Apothecia numerous and often confluent, immarginate, convex to ± globose, black, matt or slightly glossy, rarely brown (shade forms), 0·15–0·3(–0·4) mm diam. *Hymenium* 35–50 μm tall; upper part (epithecium) sordid green, K–, HNO_3+ red, or sometimes brownish in part; middle part dilute aeruginose or olivaceous; lower part dilute reddish brown and merging ± imperceptibly into the hypothecium. *Asci* clavate, 35–50×11–12 μm. *Spores* oblong-ellipsoid to fusiform, sometimes slightly curved, simple or 1–3-septate, (10–)12–21(–25)×(3·5–)4–5 μm. *Paraphyses* numerous, branched and sometimes anastomosing, *c.* 1–1·5 μm wide in mid-hymenium but upper 5–15(–25) μm thickened with dark greenish pigment and then 1·5–2·5(–3) μm wide. *Hypothecium c.* 70–140 μm tall, mottled reddish brown, K–, HNO_3– or turning orange-brown (never with purple tinge); hyphae interwoven but becoming vertically orientated towards the hymenium, hyaline or sometimes loosely coated with brown pigment, *c.* 1·5–1·7 μm wide; ascogenous hyphae with swollen cells up to 5 μm wide. *Excipulum* reflexed but distinct, reddish brown but darker than the hypothecium; hyphae radiating, branched and anastomosing, 1–1·5(–2) μm diam, hyaline (pigment confined to gel-matrix).

Pycnidia often present but very inconspicuous, immersed, 35–40 μm diam, wall dark sordid green, K–, HNO_3+ red. *Conidia* (*microconidia*) ± cylindrical, *c.* 3·5–4·7×1 μm.

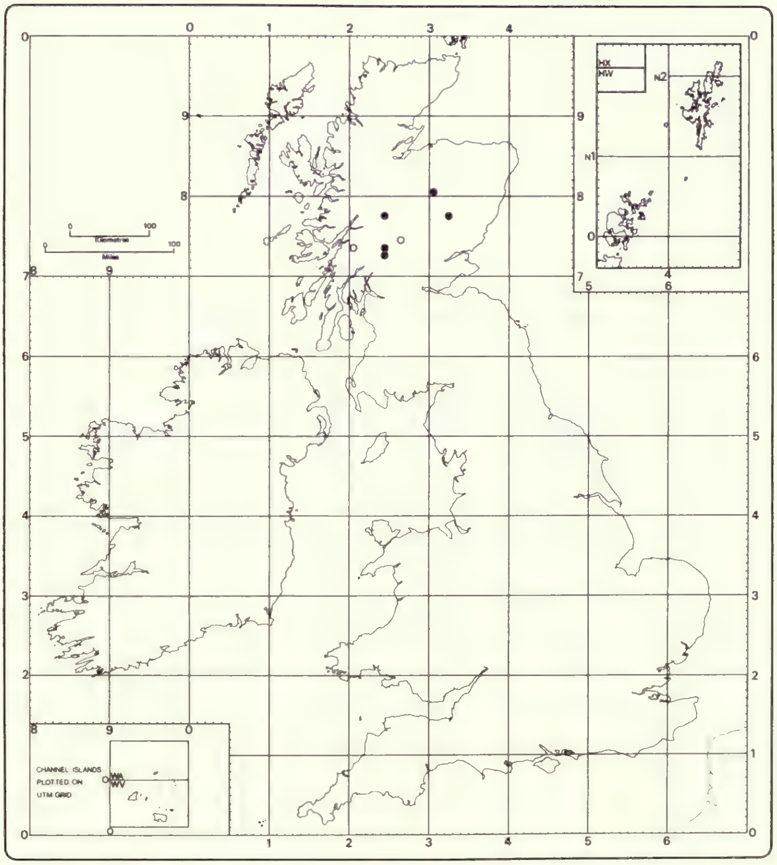
Chemistry: Sections of thallus and apothecia K–, C–, PD–; no substances detected by t.l.c.

Observations: M. turfosa is fairly constant in appearance, except that the thallus is less well developed when in boggy habitats. Microscopically there is much variation between collections with regard to spore septation: some having mostly simple spores (e.g. Vězda *Lich. Sel.* 538), others having numerous 1-septate and several 2- or 3-septate spores (e.g. Vězda *Lich. Sel.* 1135). In the type of *Biatora turfosa* the spores are mostly simple but a few with a single septum were found. In the type collections of *Biatora turfosa* verrucula* most spores are 1-septate.

With the combination of blackish thallus and black, convex to ± globose apothecia, *M. turfosa* is easily confused in the field with peat inhabiting forms of *M. melaena*, but the latter differs microscopically in having dark purple and/or green pigments in the hypothecium and thinner paraphyses. *M. botryoides* has similar apothecial pigmentation to *M. turfosa*, but its hypothecium is darker with nearly all the hyphae densely coated with pigment; in addition, *M. botryoides* has less numerous and (when hyaline) thinner paraphyses, a shallower hymenium, smaller spores, and its apothecia are always accompanied by numerous, stalked, black pycnidia. *M. melaenida* is unlikely to be mistaken for *M. turfosa* because of its whitish thallus and habitat of fine-grained, mineral soils; it can be further distinguished by its purple-brown epithecium, excipulum, and (usually) upper hypothecium. The little known *M. osloensis* differs from *M. turfosa* in several features but is most easily distinguished by its much smaller, non-septate spores.

Habitat and distribution: M. turfosa seems to have an arctic-alpine distribution. In Britain it is known from summits in the Cairngorm, Grampian, and Breadalbane mountains of Scotland, where it grows on exposed turf (mostly over dead bryophytes) at altitudes of about 860–1245 m. In the Sudeten and Carpathian mountains of Czechoslovakia it is reported at altitudes of 1400 m and 1870 m respectively. It seems to be able to occur at lower altitudes in *Sphagnum*-bogs in Scandinavia, but no altitude data is given with any of the specimens seen. I have not seen any material from the Alps but it is likely to occur there.

On the Cairngorm plateau *M. turfosa* occurs amongst *Juncus trifidus*. Associated lichens on the British gatherings include *Cladonia* spp., *Lecidea caesioatra*, and *Lepraria neglecta*.



Map 27 *Micarea turfosa* ● 1950 onwards ○ Before 1950

Outside Europe *M. turfosa* is little known, but I have seen material from Greenland and northern Alaska.

Exsiccata: Flotow *Lich.* 130 (VER). Körber *Lich. Sel.* 12 (L). Magnusson *Lich. Sel. Scand.* 282 (GZU). Malme *Lich. Suec.* 865 (WIS). Norrlin & Nyl. *Herb. Lich. Fenn.* 321 (BM, M). Vězda *Lich. Sel.* 538 (BM), 1135 (BM).

Excluded taxa

Bacidia beckhausii Körber, *Parerga lich.*: 134 (1860). – *Micarea beckhausii* (Körber) Vězda in Poelt & Vězda, *Bestimmungsschl. europ. Flechten, Ergänzungsheft* I: 162 (1977). Type: Germany, 'Westphalen', *Beckhaus* (L 910, 137 1363 – lectotype!).

Bacidia miniuscula Anzi, *Cat. lich. Sondr.*: 70 (1860). – *Micarea miniuscula* (Anzi) Vězda, *in* Vězda & V. Wirth in *Folia geobot. phytotax., Praha* **11**: 100 (1976). Type: not seen.

Bacidia beckhausii must be excluded from *Micarea,* mainly on account of its excipulum structure (see p. 189 and 198).

Bacidia nitschkeana var. ***perpusilloides*** Erichsen in *Annals mycol.* **41**: 206 (1943). Type: West Germany, Schleswig-Holstein: Flensburg, Forst Clusries, near Wasserleben, on *Picea* twigs, 6×1923, *C. F. E. Erichsen* (HBG – lectotype!). Paratypes: Schleswig-Holstein: Flensburg, Jerrishöer Holz, 10 vi 1928, *C. F. E. Erichsen* (HBG!); Hamburg, Wohldorfer Wald, 12 vi 1905, *C. F. E. Erichsen* (HBG!); Hamburg, Volksdorfer Wald, 19 xii 1909, *C. F. E. Erichsen* (HBG!). All on young twigs of *Picea.*

Thallus thin, green-grey. *Apothecia* minute, ± pellucid, pale brown, immarginate, *c.* 0·1–0·15 mm diam. *Hymenium,* hyaline, *c.* 30–40 μm tall. *Hypothecium* dark brown, K−, or + greenish in part, *c.* 40–45 μm tall. *Excipulum* thin, *c.* 12–15 μm wide, ± pseudoparenchymatous with cells *c.* 3·5–8×2·5–3 μm (in K), hyaline or with greenish pigment in zone adjacent to hymenium. *Asci* clavate, numerous, 8-spored. *Spores* oblong-fusiform, straight or slightly curved, 3(–5)-septate, 16–24(–28)×3–4 μm (Fig. 56A). *Pycnidia* often numerous, blackish, *c.* 50 μm diam, wall greenish in K; conidia curved or sigmoid 12–30×0·8 μm. *Phycobiont* cells *c.* 5–10 μm diam.

This variety agrees in all respects, except host substratum, with *Bacidia myrtillicola* Erichsen in *Mitt. Inst. allg. Bot. Hamb.* **10**: 414 (1939); type: Schleswig-Holstein: Lauenburg, 'im "Sachsenwald" bei Friedrichsruh an *Vaccinium myrtillus* am Rande des Reviers "Saupark".', 2 xi 1924, *C. F. E. Erichsen* (HBG – holotype!). *B. myrtillicola* belongs to the mainly foliicolous groups of *Bacidia s. lat.* that includes *B. fuscatula* (Müll. Arg.) Zahlbr., *B. rhapidophylli* (Rehm) Zahlbr., and *B. vezdae* Coppins & P. James.

Catillaria melanobola f. ***frullaniae*** B. de Lesd., *Rech. Lich. Dunkerque,* Suppl. 1: 119 (1914). Type: France, Nord, near Burgues, on *Frullania* on *Ulmus, M. B. de Lesdain,* Zahlbr. *Lich. Rar. Exs.* 152 (BM – isotype!).

This is an apparently undescribed (at specific rank) species of *Arthonia s. lat.* The apothecia are very small, *c.* 0·1 mm diam, convex-globose and black. In section the epithecium and hypothecium are brownish (K+ olive), the asci clavate, *c.* 21×10 μm at maturity, with a minute internal amyloid ring [as described for *Bryostigma leucodontis* (Poelt & Döbbeler, 1979) and *Chrysothrix* (Laundon, 1981), and noted by me in several *Arthonia* species, especially lichenicolous species and members of the subgenus *Allarthonia*], spores hyaline, 1-septate, 9–11×2·3–3 μm, and paraphyses scanty, thin, *c.* 0·6–1 μm wide. This species is rather common in the British Isles where it is usually referred to as '*Arthonia* cf. *exilis*'. It is found in a variety of habitats, for example bark of shaded trunks of *Acer, Fraxinus* and *Ulmus,* branches and twigs of *Corylus* and *Sambucus*, over bryophytes (especially *Frullania*) on trunks of *Quercus* and *Ulmus*, tufts of *Armeria* on sea-cliffs, and possibly also on sandstone rocks. When on bark the apothecia may attain a larger size, to 0·2 mm diam. Corticolous material has recently been distributed as Vězda *Lich. Sel.* 1701. In E it is represented by material from the following British vice-counties: 1, 20, 29, 31, 62, 64, 67, 78, 83, 88, 90, 98, 99, 110, H18 and H20; and from Denmark and Germany (Schleswig-Holstein).

There has been much confusion regarding the correct interpretation of *Arthonia exilis* (Flörke) Anzi. I have recently had the opportunity of examining type material of this species (Flörke *Deutsch. Lich.* 187 (WRSL – lectotype!)) and a brief description of it is as follows:

Thallus lignicolous (probably on worked timber; accompanied by a few granular-areolae of *Candelariella vitellina*), thin, grey-white. *Phycobiont* not *Trentepohlia*, cells, 10–19 μm diam. *Apothecia* numerous, ± regularly dispersed, black, 0·1–0·2 mm diam. *Epithecium* (including lower border with substratum) reddish brown, K−. *Hymenium c.* 30 μm tall, I+ reddish, K/I+ blue. *Asci* clavate, with minute amyloid ring ('*Bryostigma* – type'), 22–30×14–15 μm, 8-spored. *Spores* hyaline, 1-septate, 8–12×2·5–3·5(–4) μm. *Paraphyses* ± coherent (even in K), rather stout, *c.* 1·5–2 μm wide; apices ± swollen with brown

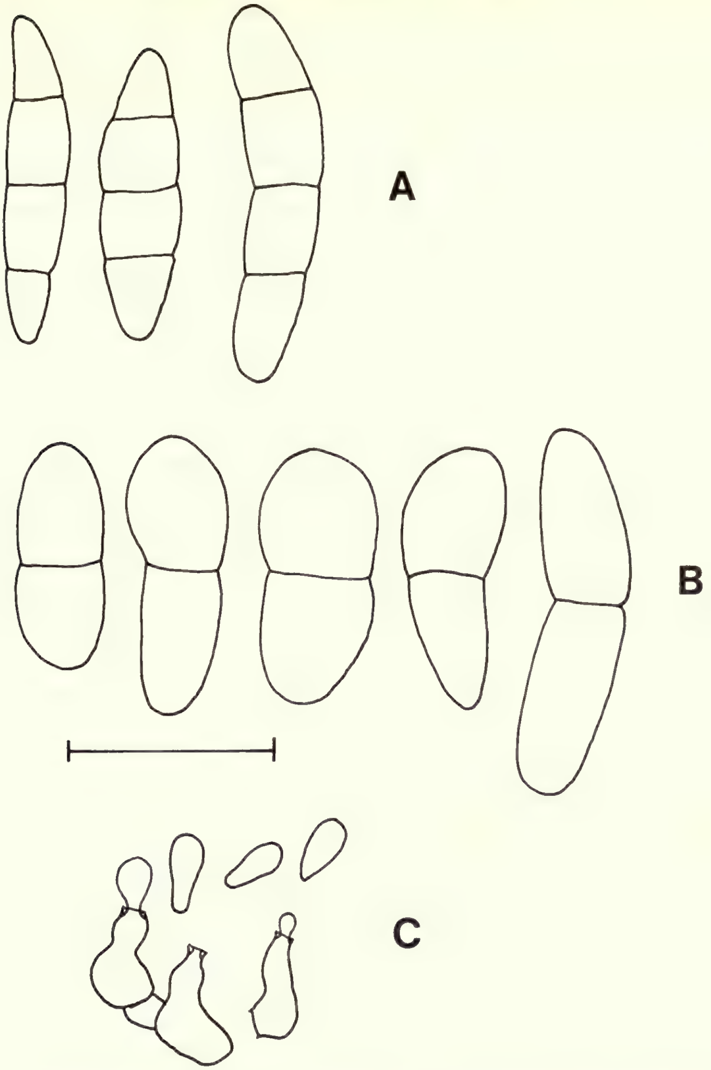


Fig. 56 **A**, spores of *Bacidia myrtillicola* (HBG – lectotype of *Bacidia nitschkeana* var. *perpusilloides*). **B–C**, *Catillaria bouteillei* (H-NYL 1884 – holotype of *Lecidea littorella*); **B**, spores; **C**, conidiogenous cells and conidia. Scale = 10 μm.

pigment-caps; closely adhering pigment sometimes continuing down to about mid-hymenium level. *Hypothecium* hyaline.

The status of *A. exilis s. str.* as a British species requires confirmation.

Catillaria rhodosphaera Th. Fr. & Hulting in Th. Fr. *Lich. Scand.* **2**: 571 (1874). Type: Sweden, Dalsland, Håverud, 1870, *J. Hulting* (UPS – lectotype!; UPS – isolectotype!).

This species was provisionally referred to *Micarea* by Kilias (1980: 392), but in fact belongs to *Biatora* Fr., a name which requires conservation against *Biatora* Ach. (= *Stenhammarella* Hertel). In my opinion *C. rhodosphaera* represents a saxicolous form of *Catillaria sphaeroides* (Dickson) Schuler.

Lecidea arceutina var. ***hypnaea*** Nyl. in *Flora, Jena* **51**: 165 (1968). – *Bacidia arceutina* f. *hypnaea* (Nyl.) A. L. Sm., *Monogr. Brit. Lich.* **2**: 158 (1911). Type: Jersey, 1866, *Larbalestier* (H-NYL 17931 – holotype!).

Based on examinations of supposed isotype material at BM, this was listed as a synonym of *Bacidia lignaria* by James (1965) and *Micarea lignaria* var. *lignaria* by Hawksworth *et al.* (1980). However, the holotype in H-NYL is a muscicolous form of the normally corticolous (occasionally saxicolous) *Bacidia* *arceutina* (Ach.) Arnold. In his diagnosis Nylander gives the spore length as 45–70 μm and on the holotype packet he wrote '45–20×1 μm'; my examination of the holotype found the spores to be 38–51×1·5 μm.

Lecidea clavulifera Nyl. – see *Psilolechia clavulifera.*

Lecidea demarginata Nyl. in *Flora, Jena* **61**: 245 (1878). Type: Finland, Tavastia australis, Evo, 'supra saxum in sylva juniori, loco olim deusto', 1873, *J. P. Norrlin*, Norrlin & Nyl. *Herb. Lich. Fenn.* 179 (H – lectotype!; isolectotypes (without exsiccate label): H-NYL 20162! & 20163!).

In the protologue Nylander cited material of Norrlin's from Finland and of Larbalestier's from Ireland. The epithet '*demarginata*' was first used in 1875 on the label of *Herb. Lich. Fenn.* 179, although without a diagnosis. An example of this exsiccate is here selected as lectotype, and is a specimen of *Lecidea erratica* Körber. The cited Larbalestier material is represented in BM and H and belongs to *M. lutulata*.

Lecidea denigrata var. ***bacidiella*** Vainio in *Medd. Soc. Fauna Fl. fenn.* 10: 28 (1883). – *Micarea bacidiella* (Vainio) Vězda, in Vězda & V. Wirth in *Folia geobot. phytotax., Praha* **11**: 100 (1976). Type: Finland, Lapponia kemensis, Sodankylä, Pyhätunturi, Kannolla, on lignum, 1878, *E. A. Vainio* (TUR-VAINIO 22505 – holotype!).

As stated by Vainio (1934: 462) this is a synonym of *Bacidia miniuscula* Anzi (i.e. *B. beckhausii* Körber). The following were notes made from the holotype of var. *bacidiella*:

Thallus lignicolous, entirely endoxylic. *Phycobiont* cells *c.* 8–14 μm diam. *Apothecia* thinly marginate and ± plane when young, soon becoming convex and immarginate, black, *c.* 0·2–0·3 mm diam. *Hymenium* *c.* 35 μm tall, with olivaceous vertical streaks, K+ violet, C+ violet (not red). *Asci* clavate, 30–35×10–12 μm, 8-spored. Spores rod-shaped or slightly curved, (1–)3(–7)-septate, 17–26×1·7–2 μm. *Paraphyses* simple or sparingly branched, 1–1·5 μm wide; apices somewhat incrassate, to 2 μm wide. *Hypothecium* hyaline. *Excipulum* dilute olivaceous (K+ violet), of radiating, branched hyphae *c.* 1·5–2 μm wide embedded in a dense gel; hyphae becoming more distinct in K but not separating. *Pycnidia* immersed in the substratum, black, *c.* 50–100 μm diam; walls olivaceous, K+ violet. *Conidia* simple, hyaline, oblong-ellipsoid, often wider at proximal end, 2·8–3·5×1(–1·4) μm.

B. beckhausii usually occurs on bark, although I have seen a few additional lignicolous specimens from Scotland. *Micarea bacidiella sensu* Vězda & Wirth (*loc. cit.*) is not *B. beckhausii* but the superficially similar *Micarea globulosella* (see p. 135).

Lecidea erysiboides Nyl. in *Not. Sällsk. Fauna Fl. fenn.* **4**: 232 (1859). – *Catillaria erysiboides* (Nyl.) Th. Fr. *Lich. Scand.* **2**: 572 (1874). Type: Finland, Nylandia, Helsingfors [Helsinki], 'Gumtackt' on rotting decorticate pine trunk, 1858, *W. Nylander* (H – lectotype!; H-NYL p.m. 4514 – isolectotype!).

This name has been misapplied by many lichenologists and the majority of specimens seen belong to *Micarea prasina,* or other species such as *Catillaria sphaeroides, Lecania cyrtella,* and *Micarea denigrata.* The type material of *L. erysiboides* is not a *Micarea* but a species of *Catillaria s. lat.*, although I am uncertain of its affinities. It has small, plane to convex, reddish brown (testaceous) apothecia that are marginate when young, the excipulum is composed of much-branched, radiating hyphae which are distinct in K but still tightly bound by the gel matrix, and the spores are ovoid and often constricted at the septum, 1-septate with the upper cell usually enlarged and ± globose, 8–9·5×3–5 μm. *C. erysiboides* has not been correctly reported from the British Isles but it should be looked for, especially in the eastern Scottish highlands.

Additional specimens of *C. erysiboides* examined: NORWAY. Hordland: Granvin, on *Betula* lignum, 1904, *Havaas, Lich. Exs. Norv.* 292 (BG). FINLAND. Nylandia: Helsinki, 1859, *W. Nylander* (H-NYL 21650), and 1861 (BM). ITALY: Trentino ('Sudtirol'): Paneveggio, on top of cut stump of *Picea*, 2 ix 1883, *Arnold, Lich. Exs.* 1002 (BM ex K). USSR. 'Lapponia orientalis', 1863, *N. I. Fellman, Lich. Arct.* 156 (BM ex K).

Lecidea fuliginea Ach., *Syn. Lich.*: 35 (1814). – *Micarea fuliginea* (Ach.) Fr., *Syst. orb.*: 257 (1825). – *Micarea fuliginea* (Ach.) Fr., *Stirp. agri femsion.*: 37 (1825); *comb. inval.* (Arts 34.1, 43).

I have not seen the type of this name but it is probably a synonym of *Lecidea icmalea* Ach. A later synonym of the latter is *Pannularia perfurfurea* Nyl. which is the type of the genus *Placynthiella* Gyelnik.

Lecidea gelatinosa Flörke in *Magazin Ges. naturf. Fr. Berl.* **3**: 201 (1809). – *Micarea gelatinosa* (Flörke) Brodo in *Bryologist* **70**: 216 (1967).

I have not seen type material of this species, but if its general interpretation is correct then it is not a *Micarea.* In fact it belongs in the *Lecidea granulosa* group, which includes *L. aeruginosa* Borrer, *L. aeneofusca* Flörke ex Flotow, *L. granulosa* (Hoffm.) Ach. and *L. viridescens* (Schrader) Ach. These species are not congeneric with the type species of *Lecidea* Ach. (*L. fuscoatra* (L.) Ach.) and they await the formal transference to a genus in the *Trapeliaceae*. Further detailed studies are needed to see if they can be placed in *Trapelia* Choisy or *Trapeliopsis* Hertel & G. Schneider, or if a new genus is required to accommodate them.

Lecidea littorella Nyl. in *Flora, Jena* **60**: 229 (1877). – *Catillaria littorella* (Nyl.) Zahlbr., *Cat. lich. univ.* **4**: 56 (1926). Type: Ireland, West Galway, 'Hibernia occidentalis, Bord du Lough Inagh, mais extremement rare', 1876, *C. Larbalestier* (H-NYL 18884 – holotype!, isotypes: BM!, BM ex K!).

The following notes were made from the holotype: *Thallus* saxicolous, not delimited but forming small patches amongst *Hymenelia lacustris* and *Porina chlorotica*, whitish, or dull ochraceous in part (? due to age), rimose, matt. *Apothecia* numerous, weakly marginate, plane to slightly convex, pallid to dull orange-red, 0·1–0·3 mm diam; margin not exceeding the level of the disc, very thin, *c.* 0·1–0·3 mm diam; margin not exceeding the level of the disc, very thin, *c.* 0·01–0·02 mm wide, whitish with faintly pruinose appearance. *Hymenium* 40–47 μm tall, hyaline. *Asci* cylindrical-clavate, '*Lecanora*-type', 8-spored. *Spores* ovoid to ovoid-oblong, often 'slipper-shaped', 1-septate and often constricted at the septum, 9·5–14(–16)×4–6(–7) μm (Fig. 56B). *Paraphyses* numerous, thin, 0·8–1 μm wide, simple or sparingly branched below, becoming wider (to 1·7 μm) and more frequently branched above. *Hypothecium* hyaline. *Excipulum* hyaline or dilute yellow-straw, inspersed with minute crystals in water mounts but ± clearing in K, *c.* 20 μm wide laterally, slightly widening below to 28 μm, minutely paraplechtenchymatous with cells in the lower part measuring 4–6×2·5–4 μm. *Pycnidia* frequent, at first immersed, later becoming emergent, white (translucent when wet), *c.* 80–100 μm diam. *Conidia* (Fig. 56C) simple, ovoid to pyriform, 2·8×1·5–1·7 μm.

L. littorella was provisionally referred to *Micarea* by Kilias (1981: 392). However, my subsequent examination of the holotype proved it to be a saxicolous form of the normally foliicolous *Catillaria bouteillei* (Desm.) Zahlbr.; previous reports of this species on rock are given by Degelius (1944) and Santesson (1952). *C. bouteillei* is apparently widely distributed in Ireland, especially on the leaves of *Buxus* (Knowles, 1929; Scannell, 1978). An additional British saxicolous specimen has been located: V.C.5, South Somerset, Broomfield, Ruborough Camp, 1914, *W. Watson* (BM ex K).

Nylander's choice of the epithet '*littorella*' is rather misleading because the holotype was not collected on the sea-shore, but on the shores of an inland, freshwater lake some 10 km from the sea. British authors (e.g. James, 1970; Fletcher, 1975) have mistakenly applied the name *Catillaria littorella* to a species that grows in crevices in siliceous rocks near the sea-shore; this species probably belongs to the perplexing *Lecania erysibe* complex.

Lecidea milliaria a. [var.] ***terrestris*** Fr. *Lich. Eur.* 342 (1831). Type: not designated.

This name is of unlikely application in *Micarea*. Fries cited his *Lich. Suec.* no. 213, the example of which in UPS is a member of the *Lecidea limosa* group.

Lecidea ocelliformis Nyl. in *Flora, Jena* **48**: 145 (1865). – *Bilimbia ocelliformis* (Nyl.) Branth. & Rostr. in *Bot. Tidskr.* **3**: 226 (1869). – *Lecidea atroviridis* f. *ocelliformis* (Nyl.) Hedl. in *Bih. K. svenska VetenskAkad Handl.* III, **18** (3): 64 (1892). – *Catillaria prasina* f. *ocelliformis* (Nyl.) Erichsen in *Annls. mycol.* **41**: 205 (1943). Type: Finland, Tavastia australis, Hollola, ad corticem *Sorbi*, 30 vi 1863, *J. P. Norrlin* 210 (H-NYL 20607! – labelled 'Isotype' by M. Inoue in 1979).

This is not a *Micarea*. If the types of *L. atroviridis* (Arnold) Th. Fr. and *L. ocelliformis* are conspecific, as placed by Hedlund (*op. cit.*) and Vainio (1934: 218), then the latter epithet has priority.

Lecidea pauxilla Krempelh. in *Verh. zool.-bot. Ges. Wien* **26**: 455 (1876). Type: New Zealand, on bark [? *Podocarpus*], 18 –, *C. Knight* (M – lectotype!; M – isolectotype!).

L. pauxilla was given as a synonym of *Catillaria synothea* (i.e. *Micarea denigrata*) by Zahlbruckner (*Cat. lich. univ.* **4**: 78, 1926). However, the type material belongs to *Cliostomum griffithii* (Sm.) Coppins.

Lecidea recondita Erichsen in *Annls mycol.* **42**: 25 (1944). Type: Germany, Schleswig-Holstein: 'Apenrade, an Blöcken am Grunde einer Erosionsschluct im Gehölz Jürgensgaard' [now Denmark, Jylland, near Åbenrå], 28 vii 1932, *C. F. E. Erichsen* (HBG – holotype!).

In the protologue Erichsen compares this with *Lecidea sylvicola* (= *Micarea sylvicola*). My examinations of the holotype proved it not to be a *Micarea* but referable to *Catillaria chalybeia* (Borrer) Massal.; see Kilias (1980: 448).

Lecidea sabuletorum f. ***simplicior*** Nyl., *Lich. Scand.*: 205 (1861). – *Bilimbia trisepta* f. *simplicior* (Nyl.) Vainio in *Acta Soc. Fauna Fl. fenn.* **53** (1): 258 (1922). Type: not designated.

Nylander (*loc. cit.*) cited the following material 'supra muscos ad Helsingforse [ipse] et in Sueciae montibus [Thedenius] atque supra terram in Lapponia'.

According to Fries (1874: 523) the 'Helsingforse' specimen is *Lecidea verrucula* (= *Micarea turfosa*); according to Vainio (1922: 140) the Swedish specimen from Funnesdalsberget in Härjedalen collected by

K. F. Thedenius is *Lecidea dufourei* (= *Catillaria contristans* (Nyl.) Zahlbr.). I am uncertain as to the identity of the specimen(s) referred to by Nylander as 'in Lapponia'. This may be based on the specimen cited by Vainio (1922: 140, 258) as 'supra Grimmias in Kipinä Lapponiae a G. Selin collecta', which Vainio refers to *Bilimbia trisepta* [sensu Vainio = *Micarea peliocarpa*] f. *simplicior*. However, material in Nylander's herbarium (H-NYL 18841) labelled 'Lapponia, G. Selin 1861' is *Catillaria contristans*. Furthermore, another specimen of '*Lecidea sabuletorum* f. *simplicior*' collected from Iceland by Isaac Carroll in 1861 (H-NYL 18862) is also *C. contristans*. It would appear that Nylander's concept of '*simplicior*' is best fitted by *C. contristans* and should be typified on the material collected by Thedenius or Selin.

Lichen niger Hudson, *Fl. angl.*, ed. 2, **2**: 524 (1778). – *Collema nigrum* (Hudson) Hoffm., *Deutschl. Fl.*: 103 (1796). – *Micarea nigra* (Hudson) Fr., *Syst. orb.*: 257 (1825). – *Micarea nigra* (Hudson) Fr., *Stirp. agri femsion.*: 37 (1825); *comb. inval.* (Arts 34.1, 43). – *Placynthium nigrum* (Hudson) Gray, *Nat. Arr. Br. Pl.* **1**: 395 (1821).

This is the type species of the genus *Placynthium* Gray.

Lichen viridescens Schrader, in Gmelin *Syst. nat.* **2** (2): 1361 (1792). – *Lecidea viridescens* (Schrader) Ach. *Meth. Lich.*: 62 (1803). – *Micarea viridescens* (Schrader) Brodo in *Bryologist* **70**: 216 (1967).

I have not seen the type of this name but if its normal interpretation is correct then the species belongs to the *Lecidea granulosa* group; see notes above under *Lecidea gelatinosa*.

Micarea chrysophthalma P. James in *Lichenologist* **5**: 131 (1971). – *Chrysothrix chrysophthalma* (P. James) P. James & Laundon, in Laundon in *Lichenologist* **13**: 104 (1981).

This is a species of *Chrysothrix* and is discussed in detail by Laundon (1981).

Micarea coccinea Fr., *Syst. orb.*: 257 (1825); *nom. nudum* (Art. 32.1).

I do not know the identity of this species, and I have not seen this name in any other publication. On morphological grounds it is unlikely that Fries intended a new combination based on *Lichen coccineus* Dickson [= *Haematomma ochroleucum* (Necker) Laundon] or *Lecidea coccinea* Schw. [= *Lecidea russula* Ach.].

Micarea cyanescens Poelt & Döbbeler in *Bot. Jb* **96**: 339 (1975). Holotype: Germany, Bayern, Altbayerische Alpen, Chiemgauer Berge, 900–1000 m on *Campylium halleri* on north-facing calcareous rocks, 29 ix 1974, *J. Poelt* (GZU, not seen). Paratypes: Austria, Tirol, Lechtaler Alpen, 'unteres Medriol-Tal über Zams bei Landeck, an Dolomitblöcken unter Grünerlen', 1600–1700 m, on *Campylium halleri*, 1969, *J. Poelt* (hb Poelt 13295!); Austria, Steiermark, 'über Kalk, Rote Wand bei Mixnitz, *c.* 1470 m, unweit des Gipfels', 1974, *J. Poelt* (GZU!).

This is a very curious species; its hymenium components are embedded in a dense gel which does not disperse in 50% of KOH. It is not a *Micarea* and a new genus is probably required to accommodate it.

Micarea hylocomii Poelt & Döbbler in *Bot. Jb.* **96**: 341 (1975). Type: Austria, Tirol, Samnaun Gruppe, on the way from Serfaus to Madatschen, *c.* 1500 m, on *Hylocomium splendens*, 15 ix 1972, *J. Poelt* (GZU – holotype!).

I endorse the describing authors' view that the position of this species in *Micarea* is doubtful, and I believe a new genus should be erected to accommodate it.

Micarea leprosa P. James in *Lichenologist* **5**: 133 (1971). – *Vezdaea leprosa* (P. James) Vězda, *in* Poelt & Döbbeler in *Lichenologist* **9**: 170 (1977).

This is a species of *Vezdaea* (Poelt & Döbbeler, 1975). A large collection of it from Scotland has recently been distributed as Hertel *Lecid. Exs.* 60.

Micarea minima Poelt & Döbbeler in *Bot. Jb.* **96**: 342 (1975). Holotype: Germany, Rheinland-Pfalz, 'Böschung eines Waldweges bei Battweiler, Kreis Zweibrücken, *c.* 400 m', on *Polytrichum commune* and *P. formosum*, 1974, *J. Poelt* (GZU, not seen). Paratype: Austria, Kärnten, Nockgruppe, Afritzer Berge, 'Bergwald und saure Weiden über Verditz, nördlich Villach', *c.* 1300 m, on *Polytrichum formosum*, 1974, *J. Poelt* (hb Poelt 13294!).

I was unable to find any apothecia in the examined paratype and so I cannot confidently exclude this species from *Micarea*. Further studies are required to establish its generic disposition.

Patellaria nigrata Müll. Arg. in *Flora, Jena* **71**: 540 (1888). – *Bacidia nigrata* (Müll. Arg.) Zahlbr., *Cat. lich. univ.* **4**: 129 (1926). – *Micarea nigrata* (Müll. Arg.) Kalb, *Lichenes Neotropici* Fasc. **1**: 8 (1981); *comb. inval.* (Art. 33.2). Type: Brazil, Apiahy, on argillaceous soil, 1883, *Puiggari* (G!).

This species closely resembles a *Micarea* and even appears to have 'micareoid' algae. However, its excipular hyphae are conglutinated, broad (*c.* 2–2·5 μm in K), and pachydermatous. It is closely allied to *Bacidia subrudecta* (Vainio) Zahlbr. and may have affinities with *Byssoloma*, but I think it is best retained in *Bacidia s. lat.* pending further study. The material distributed by Kalb (*Lich. Neotrop.* Exs. 22) as '*Micarea nigrata*' is *M. lignaria* var. *lignaria*.

Psilolechia clavulifera (Nyl.) Coppins, **comb. nov.** – *Lecidea clavulifera* Nyl. in *Flora, Jena* **52**: 294 (1869). – *Micarea clavulifera* (Nyl.) Coppins & P. James, in D. Hawksw., P. James & Coppins in *Lichenologist* **12**: 107 (1980). Type: Finland, Lapponia kemensis, Muonionska [Muonio], Keimiöniemi, ad radicem abietis, 1867, *J. P. Norrlin* 627 (H – lectotype!; isolectotypes: H!, H-NYL 20855!).

Lecidea clavulifera f. *subviridicans* Nyl. in *Flora, Jena* **60**: 463 (1877). Type: Ireland, West Galway, Connemara, Kylemore, in a cave on the NW side of Doughraugh mountain, 1876, *C. Larbalestier* (BM – lectotype! Isolectotypes: BM ex K!; also distributed as Larbal. *Lich. Herb.* 29: BM!, H!).

Thallus effuse, whitish or greenish white, of dispersed to coalescing, irregular granular-areolae *c.*

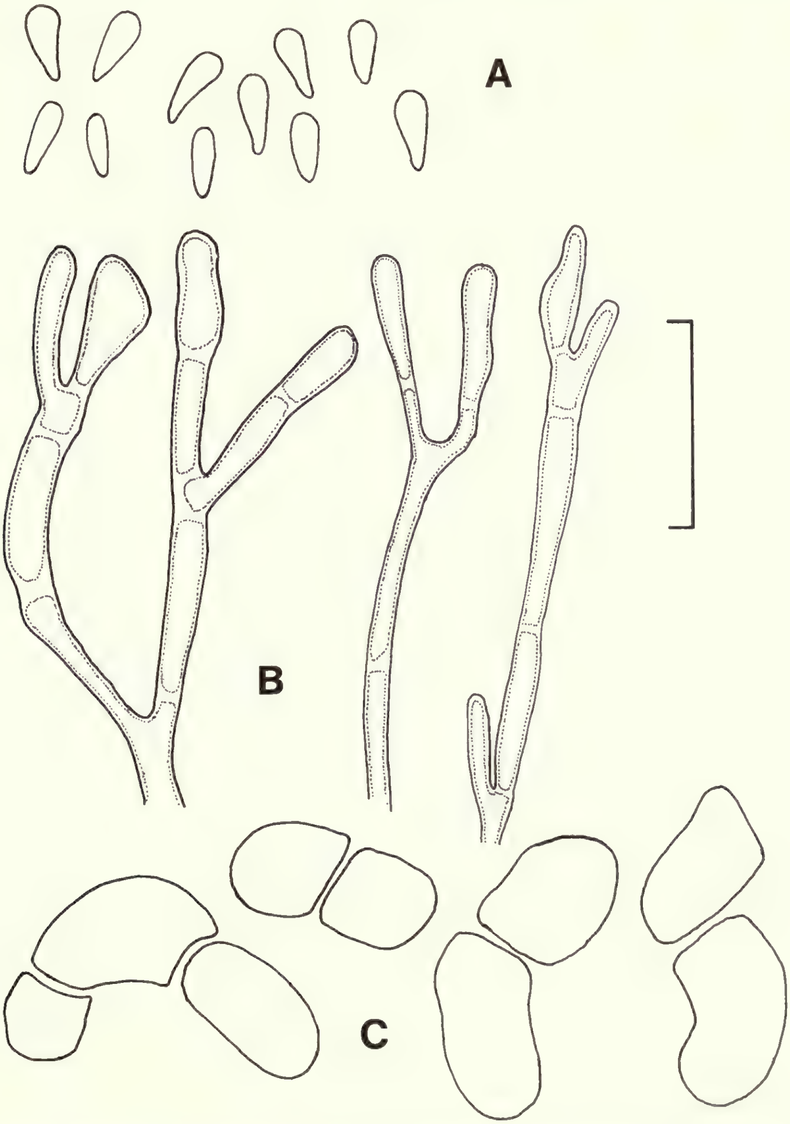


Fig. 57 *Psilolechia clavulifera* (*Coppins* 3614, E). **A**, spores. **B**, paraphyses. **C**, phycobiont cells (cell contents and mycobiont hyphae omitted). Scale = 10 μm.

0·1–0·2 mm diam. Areolae often disintegrating to form a scurfy-granular crust. *Phycobiont* not micareoid; cells in clusters and tightly bound by short-celled hyphae, but haustoria not observed; clusters interconnected by filamentous hyphae *c.* 1·5–2 μm wide. Phycobiont cells irregularly globose, broadly ellipsoid or oblong, *c.* 5–12(–18)×3–8 μm, often arranged in pairs or in short chains of up to four cells (Figs. 57C).

Apothecia convex-hemispherical and immarginate from the beginning, sometimes becoming subglobose, more rarely tuberculate, grey-black with bluish tinge, but shade forms sometimes whitish, blue-grey or grey-brown, 0·1–0·3(–0·4) mm diam; base of apothecia with a white rim (*c.* 50 μm wide) of outwardly radiating hyphae. *Hymenium* 28–35 μm tall, dilute straw (shade forms), or dilute greenish or aeruginose (K+ green intensifying) especially in the upper part. *Asci* cylindrical-clavate, 25–30×5–7 μm, 8-spored. *Spores* ovoid, oblong-ovoid or dacryoid, simple, 3–6×(1–)1·2–1·7(–2) μm (Fig. 57A). *Paraphyses* (Fig. 57B) numerous, usually branched, sometimes anastomosing, distinctly septate and appearing ± articulated, stout, 1·3–2 μm wide; apices sometimes ± clavate and up to 3 μm wide, walls not pigmented but often surrounded by deeply pigmented gel matrix. *Hypothecium c.* 50–70 μm tall, hyaline, or dilute greenish or aeruginose (K−, HNO_3+ red) but then never darker than the hymenium. *Excipulum* indistinct, of radiating hyphae that protrude as loose, hyaline hyphae *c.* 1·5–2 μm wide and up to 50 μm long.

Pycnidia not found.

Chemistry: All parts K−, KC−, C−, PD−; no substances detected by t.l.c.

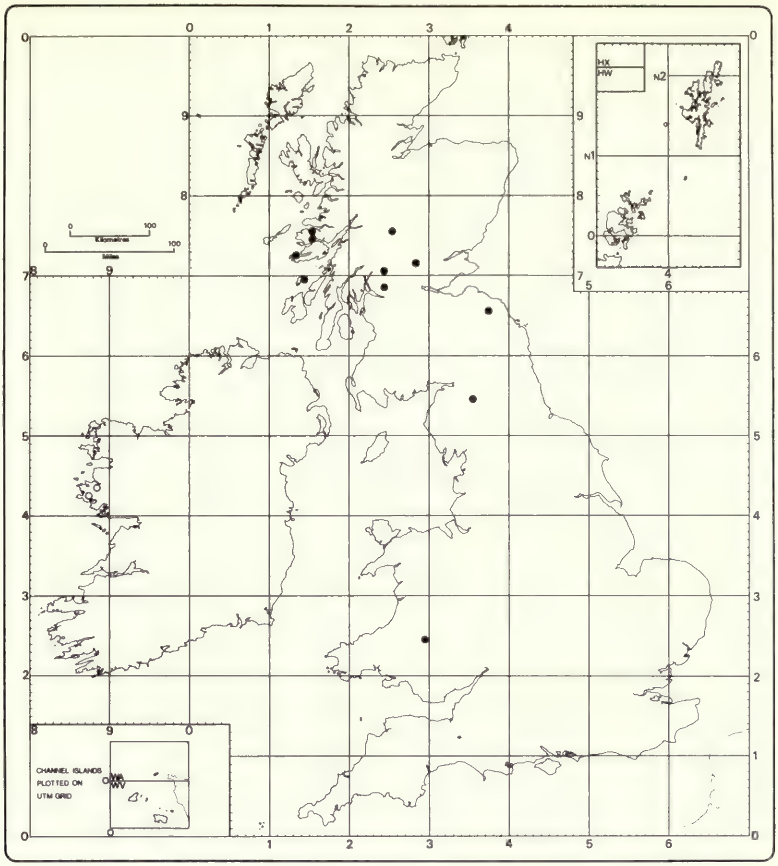
Preliminary studies of *Lecidea clavulifera* by Mr P. W. James and myself led us to transfer it to *Micarea*. However, critical studies have given me second thoughts on this placement. The distinct white rim of protruding excipular hyphae (superficially like those of *Byssoloma* spp.), stout and distinctly septate paraphyses, and the unusual phycobiont are all uncharacteristic of a *Micarea*. The consideration of *Psilolechia* Massal. as an alternative genus for *L. clavulifera* was prompted by observations of a lichenicolous member of the Caliciales, *Microcalicium arenarium* (Hampe ex Massal.) Tibell; *M. arenarium* is usually found as a parasite of *Psilolechia lucida* (Ach.) M. Choisy (see Tibell, 1978), but at three localities in Scotland I have found it on *L. clavulifera*. At the Berwickshire locality the host and parasite occurred in abundance on roots, stones, and soil of two up-ended trees (*Fraxinus*); *P. lucida* was also present in quantity but was not parasitized by *M. arenarium*.

With the exception of pigmentation, sections of the ascocarps of *P. lucida* and *L. clavulifera* show ± identical anatomical features, e.g. nature of paraphyses, size and shape of asci and spores, and excipulum with numerous protruding hyphae. *P. lucida* differs from *P. clavulifera* in the yellow-green colour of its leprose-granular thallus and apothecia (due to presence of pulvinic acid derivatives), and a different phycobiont with ± globose cells 5–14 μm diam. The thallus hyphae of both species are identical in appearance, and pycnidia are not known in either species. A recent account of *P. lucida* is given by James (in Poelt & Vězda, 1981). The phycobiont of *P. clavulifera* is very unusual; it is reminiscent of the *Stichococcus* phycobiont of species such as *Chaenotheca stemonea* and *Coniocybe furfuracea*, but its cells are much larger.

P. clavulifera occurs in communities of the *Micareetum sylvicolae*, on roots, stones, and consolidated soil of underhangs on banks or the root systems of up-ended trees. Most British records are from Scotland, but it is also known from Cumbria, south Wales and western Ireland (Map 28). From outside Britain I have seen material of it from Finland, Germany, and Czechoslovakia (see below).

Additional specimens of *P. clavulifera* examined: BRITISH ISLES. **Brecon** (V.C.42). 22/94: Upper Dyfnant Valley, 1982, *Woods* (hb Woods). **Cumberland** (V.C.70). 35/54: Baron Wood, by River Eden, 60–75 m dry sandstone cliff, 1979, *Coppins* 4344 (E). **Berwick** (V.C.81). 36/76: W of Elba, S side of Whiteadder Water, exposed roots of up-ended *Fraxinus*, 1981, *Coppins* 8890 (E – *Microcalicium arenarium* folder). **West Perth** (V.C.87). 27/40: Aberfoyle, the Trossachs, on stone amongst roots of up-ended tree, 1978, *Coppins* 3661 (E). **Mid Perth** (V.C.88). 27/55: Black Wood of Rannoch, stone in bank by track, 1976, *Coppins* 4654 (E); 27/81: Crieff, Drummond Wood, roots and sandstone of up-ended tree, partly parasited by *Microcalicium arenarium*, 1978, *Coppins* 3164, 3625 (E). **Angus** (V.C.90). 37/33: Sidlaw Hills, Auchterhouse Hill, 396 m, underside of boulder, 1975, *Coppins* 846 (E – *Microcalicium arenarium* folder). **South Ebudes** (V.C.102). 16/49: Colonsay, Coille Mhór, roots and soil of up-ended *Betula*, 1981, *Coppins* 8878 (E). **Mid Ebudes** (V.C.103). Mull: 17/32: Bunessan, Ardfenaig Woods, 1970, *James* (BM); 17/54: Salen, 1968, *James* (BM); 17/55; Aros House, roots of up-ended tree, 1968, *James* (BM). **West Galway** (V.C.H.16). 84/72 (L/65): Connemara, near Clifden, 1878, *Larbalestier* (BM).

FINLAND. Satakunta: Siikainen, Vuorijärvi, Vääsaneva, sandy soil amongst roots of *Picea*, 1936, *Laurila* (GZU, H). W. GERMANY. Baden-Württemberg: Heidelberg, Königstuhle, on sandstone, 1883, *Zwackh* (H-NYL p.m. 4229). CZECHOSLOVAKIA. Slovakia, Nízke Tatry, Liptovská Teplička, Dzurova, 18–, *Lojka* 4289 (BM).



Map 28 *Psilolechia clavulifera* ● 1950 onwards ○ Before 1950

Sporacestra Massal. in *Atti R. Ist. veneto Sci.* III, **5**: 264 (1860). Type species: *Biatora prasina* Tuck. & Mont. in Mont. (1857), non (Fr.) Trevisan (1856).

Sporacestra was included as a synonym of *Micarea* by Vězda & Wirth (1976: 99) who confused the two quite separate applications of the name *'Biatora prasina'*. The name *Biatora prasina* Tuck. & Mont. was introduced for a corticolous species from Venezuela with long acicular spores, and no reference was made to the *'prasina'* of Fries. Similarly, Massalongo made no reference to Fries' name and his generic description (e.g. '. . . sporidii capillari aghiformi, lineari allungati . . .') clearly refers to the stated type species, '*Biatora prasina* Mont., Tuck.'.

The Venezuelan species was transferred to *Bacidia* de Not. by Zahlbruckner, but his use of the epithet *'prasina'* is contrary to the present Code. From the descriptions of this species I believe it should be retained in *Bacidia*, pending further study. The nomenclature and required new combination for the species is as follows:

Bacidia prasinata (Tuck.) Coppins, **comb. nov.** – *Biatora prasinata* Tuck. in *Syn. N. Am. Lich* **2**: 41 (1888); *nom. nov.* – *Bacidia prasina* Tuck & Mont. in Mont. in *Annls Sci. nat.* IV, **8**: 296 (1857), non (Fr.) Trevisan (1856). – *Bacidia prasina* Zahlbr., *Cat. lich. univ.* **4**: 253 (1926); *nom. illeg.* (Art. 11). Type: Venezuela, on bark, *Fendler* (not seen).

Index to exsiccatae

I have attempted to examine at least one example of all European and North American material referable to *Micarea* and distributed in recognized exsiccatae (Lynge 1915–22, 1939; Sayre, 1969). My preliminary list was compiled from Lynge (*op. cit.*), available schedae, major floras (e.g. Fries, 1874; Körber, 1855, 1859–65; Smith, 1926; Vainio, 1922, 1934) and numerous other papers dealing with species here included in *Micarea*. Most examples gleaned from these sources have been seen; the few not seen are listed after the main index. Herbarium locations for examined examples containing *Micarea* species can be found in the relevant taxonomic accounts; locations of examples not containing *Micarea* species are given in the index. The names on the exsiccate labels are given (in round brackets following the number) where they are taxonomically at variance with the species represented.

In many cases, only one or two examples of a particular number have been seen by me, thus this index must be regarded as provisional. Some numbers listed as not containing a *Micarea* (e.g. Zwackh *Lich. Exs.* 778) may well in further examples (not seen by me) contain a *Micarea*. In addition, some *Micarea* species may have been misidentified and distributed under names not connected with *Micarea*, and consequently overlooked in the course of this study.

It should be noted that many numbers in the exsiccatae of Harmand (*Lich. Loth.*), Mougeot & Nestler, and Schaerer are notoriously heterogeneous with regard to species composition, substratum, and locality. Most numbers in other exsiccatae are reasonably uniform in these respects but heterogenicity sometimes arises in cases where species of similar outward appearance occur together in the field (e.g. *M. bauschiana–M. lutulata–M. sylvicola–M. tuberculata*, and *M. denigrata–M. lignaria–M. peliocarpa*). During the preparation of exsiccatae the need for the careful identification of *individual* samples is paramount *before* they are distributed.

Generic names are abbreviated as follows: *Bacidia* (*B*), *Biatora* (*Bi.*), *Biatorina* (*Biat.*), *Bilimbia* (*Bil.*), *Catillaria* (*C.*), *Lecanora* (*Lec.*), *Lecidea* (*L.*), *Micarea* (*M.*), *Psilolechia* (*P.*) and *Scoliciosporum* (*S.*).

ANZI, Lich. Exs. Ital.: 256 *M. denigrata*; 259A (*Bil. lignaria*) *M. melaena*; 259B (*Bil. hypnophila* – given by Lynge as *Bil. lignaria*) *B. sabuletorum* (BM).

ANZI, Lich. Lang.: 148 (*Bil. syncomista*) *M. lignaria*, one example in BM with a little *M. peliocarpa*.

ANZI, Lich. Sondr.: 170A *M. peliocarpa*; 170B *M. melaena*.

ARNOLD, Lich. exs.: 120 *M. bauschiana*; 167A (*Bil. lignaria* β *saxigena* Leighton) *M. peliocarpa*; 167B *M. peliocarpa*; 217 *M. nitschkeana*; 279, 280A–C *M. prasina*; 332A–C *M. melaena*; 348A, B *M. lignaria*; 409A *M. sylvicola*; 409B (*L. sylvicola*) *M. sylvicola*, or *M. lutulata*; 503A–D *M. nitschkeana*; 548, 549 *M. cinerea*; 556[A], B (*L. assimilata*) *M. crassipes*; 626, 627 *M. misella*; 836 *M. lithinella*; 837 *M. peliocarpa*; 1051 (*Bil. ternaria*) *M. peliocarpa*; 1057 *M. tuberculata*; 1121 *M. crassipes*; 1122 *M. prasina*; 1471 *M. elachista*; 1472 *M. prasina*.

ARNOLD, Lich. Mon.: 46 *M. denigrata*; 47 *M. cinerea*; 48 *M. nitschkeana*; 49 *M. melaena*; 115, 116 *M. cinerea*; 118 (*Bil. trisepta*) *M. peliocarpa*; 172 *M. misella*; 241 *M. misella*; 243 *M. prasina*; 244 (*Biat. prasiniza*) *M. adnata*; 245 *M. prasina*; 246 *M. elachista*; 248, 249 *M. melaena*; 269 (*Bil. trisepta*) *M. peliocarpa*; 270 (*Bil. trisepta*) *M. nitschkeana*; 307 *M. misella*; 357 (*Bil. trisepta*) *M. peliocarpa*; 407 *M. melaena*; 482 (*Bil. trisepta*) *M. peliocarpa*.

BOHLER, Lich. Brit.: 85 (*L. viridescens*) *M. lignaria*.

BRITZELMAYR, Lich. exs.: 174 (*Biat. prasiniza* var. *laeta*) *M. adnata*; 175 (*Biat. glomerella*) *L. viridescens* (M); 208 *M. misella*; 310 (*Biat. synothea*) *L. turgidula* + *Lec.* sp. (H); 464 (*Biat. synothea*) *M. denigrata* + *C. nigroclavata* (H); 599 (*Biat. synothea*) *Arthonia vinosa* (H); 829 (*Bil. milliaria* f. *nigrita*) *M. nitschkeana*; 846 *M. cinerea*; 946 *M. melaena*; 961 (*L. assimilata* f. *irrubata*) *L. hypnorum* + *L. limosa* (H).

CLAUDEL & HARMAND, Lich. Gall.: 43 *M. lignaria*; 89 *M. nitschkeana*; 445 *M. misella*.

CROMBIE, Lich. Brit.: 174 (*L. misella*) *M. misella* +/or *M. prasina*.

CUMMINGS, Decad. N Amer. Lich. Ed. I: 302 *M. lignaria*; 355 *M. prasina*. Ed. II: 232 *M. lignaria*.

ELENKIN, Lich. Ross.: 189 *M. misella*.

Erb. Critt. Ital., ser. I: 198 (*C. synothea*) *C. nigroclavata* (UPS).

FELLMAN, Lich. Arct.: 159 *M. melaena*; 164 (*L. assimilata* f. *alpestris*) *M. incrassata*, + a little *M. crassipes* in example in H; 165 (*L. assimilata*) *M. crassipes*; 166 (*L. limosa*) *M. incrassata*.

FLAGEY, Lich. Franche-Comté: 137 (*Bi. synothea*) *Lec.* sp. + *Lecidella* ? *euphorea* (UPS).

Flora Hung. exs.: 714 *M. melaenida*.

FLOTOW, Lich. exs.: 129A *M. lignaria*; 129B (*L. milliaria* b. *major* – according to Lynge) *Mycoblastus affinis* (UPS); 129C (*L. milliaria* var. *lignaria* – according to Lynge) *M. melaena*; 129D (*L. milliaria*) *C. globulosa* (UPS); 129E *M. lignaria*; 130 *M. turfosa*; 131 *M. lignaria*; 171A *M. sylvicola*.

FRIES, Lich. Suec.: 29 *M. lignaria*, + some *M. denigrata* in example in UPS; 98 *M. denigrata*, + some *M. lignaria* in example in E; 212A, B *M. melaena*.

HANSEN, Lich. Groenl.: 172 (*L. assimilata*) *L. stenotera* (BM); 247 (*L. assimilata*) *L. limosa* (BM).

HARMAND, Guide Elém. Lich.: 91 *M. lignaria*.

HARMAND, Lich. Loth.: 810 (*Lecidea vernalis,* and f. *prasina*) mixture from several localities, example in ANGUC has *Bi.* (? *Moelleropsis*) *humida, C. sphaeroides, L. icmalea* and *L. vernalis*, that in UPS has *C. sphaeroides* and *L. vernalis*; 838 *M. denigrata*; 852 *M. lignaria*; 853 *M. nitschkeana*.

HAVAAS, Lich. Norv.: 139 *M. subviolascens*; 555 *M. lignaria*; 571 (*L. sylvicola* var.) *M. lutulata*; 694 *M. subviolascens*; 710 *M. subviolascens*.

HAVAAS, Lich. Norv. Occid.: 269 *M. subviolascens*.

HEPP, Flecht. Eur.: 14 *M. denigrata*; 20 (*Bi. lignaria*) *M. nitschkeana*; 21 (*Bi. cinerea*) *M. cinerea*, or *M. nitschkeana*; 278 *M. prasina*; 284 *M. peliocarpa*; 285 (*Bi. lignaria* var. *milliaria*) *M. peliocarpa*; 504 *M. melaena*; 510 *M. peliocarpa*; 524 (*Bi. asserculorum*) *S. umbrinum* (E).

HEPP, Zürich: 206 (*L. cinerea*) *M. peliocarpa*; 210 (*L. synothea*) *Lecania cyrtella* agg. (BERN); 224 *M. prasina*.

HERTEL, Lecid. exs.: 34 *M. lignaria*; 54 *M. ? bauschiana*.

JOHNSON, N. Engl. Lich. Herb.: 373 *M. denigrata*; 375 (*L. turneri*; listed under *Bil. lignaria* by Smith (1911, 1926)) *Bacidia sabuletorum + Toninia lobulata* (BM); 376 *M. melaena*; 434 *L. sylvicola* var. *hellbomii*) *M. sylvicola*, or *M. bauschiana*; 453 *M. lignaria*; 504 *M. bauschiana*.

KALB, Lich. Neotropici: 22 *M. lignaria* (*M. nigrata*); 186 *M. lignaria*.

KAVINA & HILITZER, Crypt. Cech.: 269 *M. sylvicola*.

KÖRBER, Lich. Sel. Germ.: 12 *M. turfosa*; 75 *M. sylvicola*; 133A (*Bil. lignaria*) *M. peliocarpa*; 133B *M. peliocarpa*; 137 (*Bi. denigrata*) *L.* (*Lecidella*) *alba* (L); 250 *M. prasina*.

Krypt. Exs. Vind.: 165 *M. peliocarpa*; 362 *M. melaena*; 658 *M. lignaria*; 1232 *M. nitschkeana*; 1532 *M. misella*; 2061 (*C. prasiniza* var. *prasinoleuca*) *Dimerella diluta* (BM, BM ex K, M); 2268 *M. assimilata*; 2561 (*C. denigrata*) *C. globulosa* (BM, BM ex K); 3153 *M. denigrata*; 3154 *M. melaenida*; 3651 (*L. misella*) *M. denigrata*; 4214 *M. misella*; 4858 *M. denigrata*.

KUTÁK, Lich. Bohem.: 205 (*L. asserculorum*) *M. denigrata*; 310 *M. prasina*; 417 *M. lignaria*, + a little *M. leprosula* in example in O; 516 *M. denigrata*; 517 *M. denigrata*.

LARBALESTIER, Lich. Caesar. Sarg.: 83 (*L. arceutina* var. *hypnaea*) *M. lignaria*; 84 *M. sylvicola*.

LARBALESTIER, Lich. Herb.: 29 *P. clavulifera*; 68 *M. bauschiana*; 223 *M. lutulata*; 227 (*L. polioides*) *M. tuberculata*, but example in LIV is *L. monticola*; 272 *M. lignaria*; 304 *M. sylvicola*; 305 *M. sylvicola* or *M. bauschiana*; 347 *M. peliocarpa*.

LEIGHTON, Lich. Brit.: 120 (*Bi. uliginosa*) *M. melaena*; 210 *M. lignaria*; 238 (*L. milliaria* var. *terrestris*) *M. lignaria*, or *M. peliocarpa*, example in MANCH has a little *M. leprosula*; 386 *M. lignaria*; 388 (*L. sabuletorum* var. *milliaria*) *M. botryoides*.

LOJKA, Lich. Hung.: 60 *M. cinerea*; 61 *M. lignaria*; 134 *M. peliocarpa*.

LOJKA, Lichenoth. Univ.: 29–31 *M. prasina*; 137 *M. nitschkeana*; 233 *M. lithinella*.

MAGNUSSON, Lich. Sel. Scand.: 134 *M. prasina*; 208 *M. leprosula*; 282 *M. turfosa*; 340 *M. nitschkeana*.

MALBRANCHE, Lich. Norm.: 287 (*L. sphaeroides* var. *lignaria*) *M. nitschkeana*; 387 (*L. sphaeroides* var. *melaena*) *M. denigrata*.

MALME, Lich. Suec.: 20 *M. rhabdogena*; 21 *M. elachista*; 22 *M. anterior*; 23, 24 *M. prasina*, 25 *M. nitschkeana*; 26 *M. eximia*; 27 *M. melaena*; 28 *M. contexta*; 125 *M. lithinella*; 145 *M. denigrata*; 169 *M. peliocarpa*; 199 *M. sylvicola*; 216 *M. assimilata*; 288 *M. lignaria*; 362 *M. crassipes*; 365 (*M. denigrata* var. *pyrenothizans*) *M. misella*; 865 *M. turfosa*.

MIGULA, Crypt. Germ., Aust., Helv.: 1 (*Bil. milliaria*) *M. lignaria* +/or *M. leprosula,* ± *M. nitschkeana*; 132 *M. denigrata*; 226 *M. lignaria*.

MOUGEOT & NESTLER, Stirpes Crypt. Vog.-Rehn.: 1329 (*L. melaena*) an example in E includes a little *M. melaena*, other collections in BM (2 sets), DBN and M (3 sets) contain a selection from the following, *Lec.* spp., *L. granulosa* agg., *L. turgidula*, *L.* sp., *M. denigrata*; 1430 *M. lignaria*.

MUDD, Lich. Brit.: 156–8 *M. lignaria*; 159 *M. melaena*; 164 (*L. prasina*) *L. viridescens* (E, BM, M); 175 *M. sylvicola*.

NORRLIN & NYLANDER, Herb. Lich. Fenn.: 145 (*L. sylvicola*) *L. conferanda* (BM, H, M); 177 *M. denigrata*; 180 *M. melaena*; 182 (*L. pelidna*) *M. intrusa* [some examples may prove to be *S. umbrinum*]; 194A, B *M. crassipes*; 314 *M. elachista*, one example H is *B. hegetschweileri*; 319A, B (*L. milliaria* var. *ternaria*) *M. lignaria*; 321 *M. turfosa*; 724 *M. elachista*; 744 *M. misella*; 745 (*L. asserculorum*) *M. denigrata*; 763, 764 (*L. tuberculata*) *M. sylvicola*.

OLIVIER, Lich. Orne: 237 *M. melaena*; 344 *M. lignaria*.

PIŠÚT, Lich. Slov.: 156 *M. lignaria*.

POELT, Lich. Alp.: 22 (*L. misella*) *M. denigrata*.

RABENHORST, Lich. Eur.: 224 (*Bi. turfosa*) *L. uliginosa* (BM ex K); 322 *M. lignaria*, example in M has some *M. peliocarpa*; 582 (*Bil. lignaria*) *M. nitschkeana*; 583 *M. nitschkeana*; 603 (*Bil. syncomista*) *M. lignaria*; 626 *M. denigrata*; 648 (*Bi. bauschiana*) *M. bauschiana*, or *M. tuberculata*; 675 (*L. sylvicola*) *L. erratica* (BM, M); 676 *M. prasina*; 733 *M. prasina*.

RÄSÄNEN, Lich. Fenn. exs.: 489 (*Bil. nitschkeana*) *B. naegelii* (LD); 512 *M. tuberculata*; 642 *M. nitschkeana*; 651, 652, 653 *M. prasina*; 672 (*L. sylvicola*) *M. sylvicola*, +/or *M. tuberculata*, +/or *M. lutulata*; 822 (*C. elachista* f. *simplicata*) *L. turgidula* (BM ex K); 963 *M. melaena*.

RÄSÄNEN, Lichenoth. Fenn.: 137 (*C. elachista* f. *simplicata*) *B. igniarii* (BM ex K); 343 *M. peliocarpa*; 344 *M. melaena*; 426 (*C. ilicis*) *M. globulosella*.

Reliq. Suza.: 42 *M. misella*.

ROUMEGUÈRE, Lich. Gall.: 87 (*L. vernalis* var. *milliaria*) *B. sabuletorum* (BM, M); 193 (*L. vernalis* var. *synothea*) *M. lignaria*; 231 *M. melaena*, but example in BM is mixture of a *L.* sp. and *Lec.* spp.; 232 *M. lignaria*; 467 (*L. melonida [melaenida]*) *Toninia aromatica* (BM).

SAMPAIO, Lich. Port.: 132 *M. denigrata*; 147 *M. lignaria*.

SCHAERER, Lich. Helv.: 196 (*L. sabuletorum* var. *lignaria*) examples labelled 'Ad ligna decorticata in alpibus' are *M. prasina*, examples labelled 'In m. Belpberg' contain one, or a mixture, of the following, *M. lignaria, M. melaena, M. peliocarpa* and *M. leprosula*; 327 (*Parmelia varia* var. *denigrata*) *L. (Lecidella) alba* (BM ex K), or *L.* aff. *cadubriae* (E).

SUZA, Lich. Bohem.: 131 *M. sylvicola*.

THOMSON, Lich. Arct.: 12 (*B. melaena*) *Toninia lobulata* (LD).

VAINIO, Lich. Bras.: 1420 *M. misella*; 1451 *M. misella*.

VĚZDA, Lich. Bohem.: 133 *M. lignaria*; 258 *M. lignaria*; 282 *M. crassipes*.

VĚZDA, Lich. Sel. exs.: 11 *M. crassipes*; 14 *M. melaena*; 90 *M. prasina*; 516 *M. lignaria*; 538 *M. turfosa*; 706 (*M. violacea*) *B. naegelii* (BM); 858 (*M. ternaria*) *M. lignaria*; 957 (*L. tuberculata*) *M. sylvicola*; 1036 *M. lignaria*; 1087 *M. cinerea*; 1088 (*M. ternaria*) *M. lignaria*; 1134 *M. elachista*; 1135 *M. turfosa*; 1341 (*M. tuberculata*) *M. sylvicola*; 1342 *M. peliocarpa*; 1380 *M. peliocarpa*; 1430 *M. denigrata*; 1467 *M. prasina*; 1595 (*M. hemipoliella*) *M. prasina*; 537 *M. melaenida*.

WEBER, Lich. Exs.: 73 *M. denigrata*.

ZAHLBRUCKNER, Lich. Rar. exs.: 110 *M. nitschkeana*; 152 (*C. melanobola* f. *frullaniae* =) *Arthonia* aff. *exilis* (BM); 174 (*L. infidula*) *L. erratica*; 175 *M. prasina*; 276 *M. turfosa*.

ZWACKH, Lich. exs.: 121 *M. lignaria*; 122 (*L. milliaria* Fr. var. ?) *M. elachista*; 276 *M. peliocarpa*; 279A (*Bi. gelatinosa* var. *minor*!) *M. bauschiana*; 279B *M. bauschiana*; 394 *M. denigrata*; 416 *M. prasina*; 417 (*Bil. nitschkeana*) *S. umbrinum* + *S. chlorococcum* (UPS); 470 *M. nitschkeana* [two labels: '*Bilimbia nitschkeana*, bei Münster in Westfalen'; or '*Lecidea nitschkeana*, bei Dolbrueck in Kreise Paderborn . . .', sometimes labelled '470 *bis*', example in M. also has *M. denigrata*]; 534 *M. nitschkeana*; 535 (*L. latens*) *M. sylvicola*; 587 *M. nitschkeana*; 590 *M. lithinella*; 591A, B, 592A–E, 593A–C *M. prasina*; 594A, B, 595 *M. bauschiana*; 596 (*L. latens*) *M. sylvicola*; 597 *M. sylvicola*; 656 *M. prasina*; 657 *M. melaena*; 675 *M. melaena*; 778 (*L. cinerea*) *L. symmicta* agg. (UPS); 780 (*L. trachona*) *M. sylvicola*; 897 *M. peliocarpa*; 898 *M. cinerea*; 900 *M. turfosa*; 919 *M. sylvicola*; 1085 *M. misella*.

Examples of the following have not been examined by me; names taken from Lynge (*op. cit.*).

BRITZELMAYR, Lich. exs.: 838 (*Bil. lignaria*); 890 (*Bil. trisepta*). FLOTOW, Lich. exs.: 112 (*L. synothea* ?). HARMAND, Lich. Loth.: 834 (*L. denigrata*). KÖRBER, Lich. Sel. Germ.: 343 (*Bil. syncomista*). LARBALESTIER, Lich. Herb.: 139 (*L. micrococca*). OLIVIER, Lich. Orne: 264 (*L. nitschkeana*). ROUMEGUÈRE, Gen. Lich. exs.: 36 (*L. vernalis* var. *synothea*); 51 (*L. vernalis* var. *milliaria*). No examples of this exsiccata have been traced; it is almost certain that it was never distributed (P. M. Jørgensen, *in litt.*). SCHADE, STOLLE & RIEHMER, Lich. Sax.: 256 (*B. trisepta*). ZWACKH, Lich. exs.: 131 (*L. glomerella* and *L. confluens*).

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The hepatics of Sierra Leone and Ghana

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Synopsis

The vegetation and hepatic flora of Sierra Leone and Ghana are briefly described. Detailed information on the distribution of 178 taxa is presented, together with notes on their ecology and taxonomy. Of these taxa, 95 have been collected in both countries, 44 are known from Sierra Leone but not Ghana, and 39 have been found in Ghana but not Sierra Leone. Many of the taxa recorded only in Sierra Leone are montane in distribution and therefore unlikely to occur in Ghana. On the other hand it is probable that most of those at present recorded only from Ghana will eventually be found in Sierra Leone.

Three new species are described and illustrated: *Cololejeunea calcarata* E. Jones and *Drepanolejeunea ankasica* E. Jones from Ghana, and *Lejeunea lomana* E. Jones from Sierra Leone. The following are placed in synonymy: *Ceratolejeunea saxbyi* Pearson (= *C. calabariensis* Stephani); *Lejeunea eplicata* Stephani (= *L. ramosissima* Stephani); *Lejeunea triquetra* Mitten and *Mastigolejeunea tarkwana* Pearson (= *Thysananthus spathulistipus* (Reinw., Blume & Nees) Lindenb.); *Prionolejeunea aberrans* Stephani (= *Lejeunea papilionacea* (Stephani) E. Jones); *Taxilejeunea nicholsonii* Pearson (= *Lejeunea grossecristata* (Stephani) E. Jones), and *Riccia undulata* S. Arnell (= *R. moenkemeyeri* Stephani).

Introduction

During the nineteenth century various botanists who collected bryophytes elsewhere in Africa made brief visits to Sierra Leone (mainly Freetown) or, less frequently, the Ghana coast, but in general they seem to have collected mosses rather than hepatics; they have left very few specimens of hepatics from either country in our large herbaria, and published records are equally scanty.

Since 1910 a number of botanists, agriculturalists, etc. (see index of collectors), some resident, some as visitors, but most with no special knowledge of bryophytes, have made small collections of hepatics, the majority of which we have identified in recent years. Some of these consist of only one–three specimens; those of Hossain, Irvine, and Richards are the most considerable, apart from Jeník's, which we have not seen in its entirety.

One of us (A.J.H.) worked in the Botany Department of Fourah Bay College, Freetown, from March to December 1966. He was engaged primarily in studying the ecology of epiphyllous hepatics, but also collected other bryophytes, to a total of about 1000 specimens.

E.W.J. collected bryophytes in Ghana from 23 January to 25 February 1971 (collecting numbers 1214–1418). Working in the Botany Department of the University of Ghana at Legon, near Accra, and with the facilities provided by the Department, he was able to visit a

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representative selection of bryophyte-rich sites ranging over the whole of southern Ghana. He collected in Sierra Leone between 28 February and 1 April 1971 (collecting numbers 1419–1579). Fourah Bay College also served as his base, but he paid brief visits to the Loma Mountains, the Kambui Hills, and the Gola Hills in the east of the country. In both countries the period February–March falls in the latter part of the dry season – an advantage in so far as the weather is favourable for travelling, but a disadvantage in that some genera of terrestrial and ephemeral species such as *Fossombronia* and *Riccia* cannot be found, and sporogonia of many other species have too often disintegrated. The early dry season (October–November) is a much more favourable time for collecting bryophytes in these climates.

Our own collections form the most substantial contribution to our knowledge of the hepatic flora of the two countries. A few specimens are still unidentified and some taxonomic problems remain to be solved, but further progress is likely to be very slow, and the residue which remains to be studied is small.

E.W.J. has cited some of his own specimens, together with a few from the small collections mentioned above, in his recent papers in the series 'African hepatics' (*J. Bryol.* **7–12**, 1972–82). No comprehensive account of the hepatic flora of any West African territory exists, and the only publication dealing exclusively with the hepatics of either Sierra Leone or Ghana is a posthumously published paper by Pearson (1931) describing a small collection made by H. H. Saxby near Tarkwa, Ghana, in 1910–11. Therefore it has seemed worth preparing a list of the hepatics of the two countries based primarily on our own collections, but incorporating information from the other sources that we have indicated; this provides a picture of the hepatic flora of two representative, but in certain respects contrasting, West African countries.

Sierra Leone

Sierra Leone lies between 6°55′ and 10°N and between 10°16′ and 13°18′W. Most of the central part of the country has a mean annual rainfall of 2500–3000 mm (100–120 ins). This increases markedly towards the coast and shows a contrasting, though less pronounced, decrease towards the north. Even the driest areas of the country receive 2000 mm – more than all except the wettest parts of Ghana and Nigeria – but the dry season is longer and more severe than in these two countries. Thus Kabala, in the relatively dry north, with a mean annual rainfall of 2285 mm, is shown by Walter & Lieth (1967) as having a 'dry' period* of four months, and Bo, representative of much of the central lowlands, with a mean annual rainfall of 2937 mm, has a 'dry' period of three months.

Much of the country is situated 'within the climatic limits of closed forest' (Cole, 1968) but, except in the Freetown Peninsula and some remote hill country in the east, no mature forest remains. Shifting cultivation prevails everywhere, but in the southern half of the country fallow farmland tends to revert to forest, whereas in the drier northern half it tends to revert to savanna. We have very little information on the bryophyte flora of this large area of farmland and its derivative vegetation; a few collections (none made by bryologists) from Njala and Bo come from the moister part of the country with 'forest' tendency, and some from Musaia, Kabala, and the Lake Sonfon area come from the drier part with 'savanna' tendency.

In his vegetation map, Cole (*op. cit.*) shows a belt of savanna woodland some 20–50 km wide along the northern and north-eastern borders of the country. The hepatic flora of this woodland is unknown but is likely to be very poor.

The Freetown Peninsula, bryologically the best known part of the country, is also the wettest. Freetown itself has an average of about 3340 mm of rain a year, but the mountain ridge which rises sharply to altitudes of 600–800 m receives more than 5000 mm. The Peninsula, however, also has the longest and most severe dry season of any part of the country, and even Number

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* Walter & Lieth plot rainfall and temperature so that 10°C on the temperature scale corresponds to 20 mm rain on the rainfall scale; a 'dry' period is one in which the precipitation curve lies below the temperature curve, thus indicating the likelihood of vegetation suffering a moisture deficit. The severity of the dry period is indicated both by the length of such periods and by the distance below the temperature curve to which the rainfall curve descends. Where only monthly mean rainfall figures, but no temperature figures are available, a crude indication of the length of dry season is given by the number of consecutive months with less than some convenient arbitrary amount of rain. Hall & Swaine (1976) use 100 mm, but a lower figure, e.g. 50 mm (approximately 2 ins) is more sensitive.

Two River, with a mean annual rainfall of 5490 mm has five consecutive months each with 50 mm or less rain (Gregory, 1965).

The mountains are still clothed with forest in which bryophytes grow with great luxuriance, but the number of species is small. The almost complete absence of *Frullania* spp. is a remarkable feature of the flora which presumably has a climatic cause. Other species which might be expected but have not been recorded are *Bazzania decrescens* subsp. *molleri, Mastigolejeunea auriculata, M. nigra, Porella subdentata,* and corticolous species of *Radula*. Despite the length of the dry season epiphyllous hepatics are abundant in deep valleys where perennial streams maintain a high local humidity, as in the Fourah Bay College Botany Reserve.

Towards the interior of Sierra Leone the general level of the land rises; much of the eastern half of the country lies above 300 m, and there are some groups of hills where the most important of the remaining areas of forest are situated. Hepatics have been collected in the Kambui Hills Forest Reserve to the north of Kenema, and in the Gola Hills to the south-east, close to the frontier with Liberia. Though the hepatic flora is probably richer than that of the Freetown Peninsula it seems to show some of the same curious limitations; thus after a day spent in the Gola North Forest Reserve E.W.J. noted 'No *Mastigolejeunea* or *Ptychocoleus* were seen, and no *Frullania*', and similarly in the Kambui Hills E.W.J. noted that holostipean Lejeuneaceae, other than *Lopholejeunea* and *Archilejeunea,* were 'almost absent', and *Frullania* 'not seen'.

In eastern Sierra Leone, near the border with Guinea, rise the Loma Mountains – the highest mountains in Africa west of Cameroon – and, smaller in extent but only about a hundred metres lower, the Tingi Hills. Both consist of undulating plateaux at 1220–1520 m, with peaks rising to about 1900 m.

Bintimani (1948 m), the highest peak of the Loma Mountains, has a small summit plateau surrounded by imposing dolerite cliffs up to 80 m high. Hepatics found on the plateau and cliffs include *Fossombronia husnotii, Gongylanthus richardsii,* which is otherwise known only from basic volcanic soils in Cameroon and Tanzania, and *Plagiochasma eximium.* Some records from Bintimani are included in a short paper by Potier de la Varde (1948) on the mosses of the Loma Mountains.

The main plateau of the Lomas is covered by grassland (the 'sub-montane shrub savanna' of Cole (1968)) which is frequently burned and therefore devoid of bryophytes, except sometimes *Anthoceros* sp., *Fossombronia* sp., *Gongylanthus ericetorum,* and various small mosses between grass tussocks. However, 'gallery' forest extends up the valleys to about 1650 m and there are also small trees and bushes on rock outcrops. The edges of the forest are punctuated in many places by very large trees of *Parinari excelsa* which evidently create 'fire-breaks' by reducing the amount of grass that can grow beneath them. The sides of these large rough-barked boles which face the grassland are well illuminated and bear a remarkable bryophyte flora which includes some species not seen in other habitats; particularly noteworthy are *Chandonanthus hirtellus* and *Conoscyphus trapezioides,* tropical montane species with wide but very disjunct distributions. The understorey of the forest has a rich flora of shade-tolerant bryophytes, amongst which *Odontolejeunea tortuosa* is conspicuous.

Exposed branches of small trees and bushes growing amongst rocks are clothed with *Usnea* spp. and other lichens, and with hepatics that include *Frullania arecae,* a pantropical montane species, *F. depressa,* first described from Mont Cameroun (Cameroon Mountain), but known from many other African mountains ranging from Ethiopia to Madagascar and South Africa, and *Lejeunea ramosissima.*

Brachiolejeunea tristis, Dicranolejeunea madagascariensis var. *madagascariensis, Marchesinia moelleriana, Ptychanthus striatus,* and *Strepsilejeunea brevifissa* are other characteristic members of the African montane flora which have been recorded; it is remarkable that *Lejeunea acuta* Mitten has not been found.

The Tingi Hills have not been visited by bryologists but it is to be expected that their flora will resemble that of the Loma Mountains; in both areas *Polytrichum commune* Hedwig has been found growing on the fringes of grass mats overlying gently sloping slabs of rock. *Sphagnum davidii* Warnstorf was discovered in the Tingi Hills by J. K. Morton and D. Gledhill in 1965.

Bryophytes have never been collected in the extensive forest reserves on the lower ground to the west and south of these two massifs.

Ghana

Ghana extends from 4°45′ to 11°10′N and from 1°12′E to 3°15′W. North of about 6°30′N in the east and about 7°45′N in the west the country is covered mainly by savanna woodland (Taylor, 1960). From this area we have only three records of hepatics – *Fossombronia* sp. (probably *F. occidento-africana*), *Mastigolejeunea auriculata,* and *Targionia hypophylla.* Though the flora is unlikely to be rich, it will doubtless resemble that of the corresponding savanna in Nigeria, characterized by the more drought-resistant Lejeuneaceae such as *Acrolejeunea emergens* and *Mastigolejeunea auriculata* on trees, and on the ground by ephemeral species that perennate either by spores or tubers (e.g. *Riccia* spp.). To the south is the forest region, to which almost all collecting of bryophytes has been confined.

Hall & Swaine (1976) recognize seven main divisions within the forest on the basis of an objective analysis of its phanerogam flora; these divisions correspond to some extent with rainfall regimes. In the south-west is a lowland area of 'Wet Evergreen' forest ('Guineo-Congolian Rain forest, wetter types', UNESCO—AETFAT vegetation map of Africa (White, in press)) which extends westwards into the Ivory Coast, with a mean annual rainfall exceeding 1750 mm. Hall & Swaine point out that it has a 'wetter rainy season' than the rest of Ghana, with the mean rainfall for some months exceeding 500 mm. Going eastwards from Ghana no other lowland region with as high a rainfall is encountered until the extreme south-east of Nigeria and Cameroon is reached. The Ankasa River Forest Reserve and Aiyinasi Agricultural Research Station are in this zone. They have a rich hepatic flora which includes *Cololejeunea cornuta* and *Trachylejeunea serrulata*, two species that have hitherto been known only from the Calabar (S.E. Nigeria)–Cameroon region.

East and north-east of the Wet Evergreen forest, and still mainly lowland, is a zone of 'Moist Evergreen' forest with 1500–1750 mm mean annual rainfall. Saxby's collections from Tarkwa, and E.W.J.'s collections from the Subri and Pra-Suhien Forest Reserves, come from this zone, while the Ochi Headwaters Forest Reserve is on its northern boundary.

Still further to the north and east is a broad zone of 'Moist Semi-deciduous' forest, the most extensive forest region of Ghana, covering the broad belt of high ground which crosses southern Ghana from south-east to north-west. Much of this zone is between 150 and 300 m above sea-level; to the north-east it is bounded by a scarp which, over much of its length, controls the boundary between forest and savanna. Hall & Swaine divide this Moist Semi-deciduous forest into a 'South-east sub-type', with 1500–1750 mm mean annual rainfall (thus not appreciably different from that of the Moist Evergreen zone) and a 'dry' period (see footnote on p. 216) of usually four consecutive months each with a mean rainfall of less than 100 mm, and a distinctly drier 'North-west sub-type', with 1250–1500 mm mean annual rainfall and a 'dry' period of usually five months. The hepatic flora of the South-east sub-type is exemplified by Aburi, Kade Agricultural Research Station, and the neighbourhood of the Tafo Cocoa Research Institute, including the Southern Scarp Forest Reserve; that of the North-west sub-type by the Bia North Forest Reserve and the Krokosua Hills.

The hepatic flora of the South-east sub-type of the Moist Semi-deciduous forest closely resembles that of the Moist Evergreen forest; a few species have been recorded from the Moist Evergreen forest but not from the Moist Semi-deciduous; probably mostly the result of insufficient collecting, but the absence of *Arachniopsis diacantha, Cephalozia fissa, Plagiochila africana,* and *Thysananthus spathulistipus* is likely to be due to climate.

The hepatic flora of the drier North-west sub-type seems to be very much poorer. The contrast was particularly striking between the corticolous flora of the crowns of emergent trees in the Aiyaola Forest Reserve near Kade (12 species) and in the Bia North Forest Reserve, where only four species – *Acrolejeunea emergens, Cheilolejeunea intertexta, Frullania ericoides,* and *Mastigolejeunea auriculata,* all drought-tolerant – were found. Here also the boles of cocoa trees were almost devoid of bryophytes, whereas near Tafo at least six species of hepatic could be found in a cocoa plantation.

In general the flora of these two zones of Moist Evergreen and Moist Semi-deciduous forest closely resembles that of southern Nigeria, as seen for example in the forest reserves around Akure and Benin. The abundant species are the same, and all but seven (i.e. about 90 per cent) of the species that have been recorded from the two Ghana zones are known from Nigeria west of the Cross River; of the other seven, five (*Cheilolejeunea trifaria, Cololejeunea dentata Prionolejeunea grata, Radula holstiana,* and *Taxilejeunea pulchriflora*) are known from east of the Cross River, either in Nigeria or Cameroon, and are likely to occur to the west.

Hall & Swaine find that within the general area of the South-east sub-type of the Moist Semi-deciduous forest certain high plateaux have a floristically distinct forest which they name 'Upland Evergreen' forest. The Atewa Hills (*c.* 730 m) is the best known of these botanically, and the only one from which bryophytes have been collected. The hepatic flora includes some montane species – *Plagiochila pectinata, Radula boryana,* and *R. stenocalyx* – which are not known from the surrounding country. One small patch of swamp forest is said to be the only site of its kind in the Atewa Hills. Between dominant *Lophira alata* and *Gilbertiodendron limba* water stands 20–30 cm deep. Tree boles and the stems of the abundant undershrubs are thickly clothed with bryophytes, amongst which ramify many small and delicate Lejeuneaceae; epiphyllous hepatics are luxuriant. At some time trial pits have been dug here to explore deposits of kaolin; hence it is referred to as the 'Kaolin Swamp' to distinguish it from other less remarkable areas of wet forest. A thunder-storm and failing light greatly curtailed E.W.J.'s collecting when he visited it; it would certainly be worth much closer examination.

The Krokosua Hills form a plateau at 450–600 m in the drier North-west sub-type of the Moist Semi-deciduous forest; although they do not carry Upland Evergreen forest, the bryophyte flora seems much richer than that of the surrounding lower ground.

In eastern Ghana a narrow line of hills rises abruptly to 760–880 m, forming the frontier with Togo. One of these hills, Amedzofe (760 m), with its spectacular waterfall, has been frequently visited by botanists, and is presumably in the Moist Semi-deciduous forest zone; although no forest now remains, the bryophyte flora of the cocoa plantations of the district closely resembles that seen near Kade and Tafo. The summit of the hill bears grassland on the flank exposed to the south and south-west, with a small patch of savanna woodland in the lee of a rock outcrop. Other higher hills further north are covered entirely by savanna and have not been visited by collectors of bryophytes. We include in this paper a few records from collections made in these hills near Klouto in Togo, only a few kilometres from the Ghana frontier.

We know of no bryophyte collections from Hall & Swaine's remaining forest-types – the 'Dry Semi-deciduous', 'Southern Marginal', and 'South-east Outlier' – but their hepatic flora is probably an impoverished version of the Moist Semi-deciduous forest flora.

The coastal belt of eastern Ghana, in which lie Accra, Legon University, and also Achimota – the seat of botanical studies in Ghana before Legon was opened – receives an average of only 630–890 mm of rain a year; it is the driest part of Ghana, though the dry season is shorter and less severe than that of the northern savanna. Little attention has been paid to the hepatics in this area, and only *Anthoceros buettneri, Notothylas* spp., *Riccia rhodesiae,* and *Ricciocarpos natans* have been recorded. Though we should expect more species to be found, they are likely to be mainly terricolous.

A botanist who has worked in the forests of other parts of tropical Africa is likely to be impressed in Ghana both by the luxuriance of the forest and the richness of the bryophyte flora, especially in the Moist Semi-deciduous forest. The total annual rainfall is relatively low, but probably exercises less influence on the bryophyte flora than the frequency, severity, and length of dry periods, and in Ghana the dry periods appear to be relatively short. Thus, to take figures from Walter & Lieth (1967), Tafo, in the Moist Semi-deciduous forest, has a mean annual rainfall of 1658 mm, and a 'dry' period of less than one month, and even Kumasi, near the border between the Moist and the Dry Semi-deciduous forest, with a mean annual rainfall of 1481 mm, has a 'dry' period of only two months. We may contrast these figures with Calabar, 3028 mm mean annual rainfall and a 'dry' period of two months, or Benin with a mean annual rainfall of 1975 mm and a 'dry' period of three months – wetter than Kumasi, but with a longer dry season.

A comparison of monthly rainfalls in the forest regions of Ghana and Nigeria shows that the two-peak rainfall regime is more pronounced in Ghana, thus tending to spread a given amount of rain over a longer period. The savanna zone of Ghana, where the rainfall is of the single peak type, also has more moderate dry seasons than comparable Nigerian savanna: e.g. Tamale, 1100 mm mean annual rainfall, four consecutive months with less than 25 mm; Minna, on the same latitude in Nigeria, 1380 mm mean annual rainfall, five consecutive months with less than 25 mm.

Nomenclature and the citation of literature

Author abbreviations follow the *Draft index of author abbreviations compiled at the Herbarium, Royal Botanic Gardens, Kew* (1980).

We have given additional bibliographic references for many of the taxa included in the catalogue; these mostly refer to descriptions more detailed than those provided in the original publications.

Apart from new synonyms, we have cited only the principal synonyms that have been used in connection with the African flora.

Nomenclature of flowering plants follows Hutchinson & Dalziel (1954–72).

Identification and the citation of specimens

Except where otherwise indicated E.W.J. has named his own collections from both countries, all other collections from Ghana, and specimens collected in Sierra Leone by Arnell, Brenan, Revell, and Richards. A.J.H. has identified his own collections, unless otherwise indicated, and the small collections from Sierra Leone housed at the British Museum (Natural History).

In general, localities are cited from west to east and from north to south; we have not cited them by administrative districts as these tend to be impermanent and have indeed undergone considerable changes in both countries during the period over which records have been accumulating. Records from hilly districts have been arranged in order of altitude, from the lowest to the highest.

Where there are numerous records of a given taxon from one locality, we have sometimes cited only a selection.

The index of collectors will usually indicate sufficiently closely the date of collection and the herbarium in which the specimen is preserved. E.W.J.'s collections are in his private herbarium except where the collecting number is followed by a herbarium abbreviation (see below); in such instances the collection is not represented in his private herbarium. ! indicates a field record unsubstantiated by a herbarium specimen; such records have been cited only when there is no possible doubt as to identity. The herbarium abbreviations used are those adopted by Holmgren, Keuken & Schofield (1981).

Abbreviations

A.R.S.	Agricultural Research Station
B.R.	Botany Reserve
F.R.	Forest Reserve
p.p.	*pro parte* – in part (where a specimen includes more than one taxon)
s.n.	*sine numero* – without a number

Index of localities

The index gives the latitude, longitude, and, in most cases, altitude of all localities mentioned more than once in the catalogue. Not all of the figures are as precise as we would wish; e.g. some of the forest reserves are of considerable area and the exact point within them at which collections were made is not recorded.

Sierra Leone

Co-ordinates are taken from 1:50,000 maps published by the Directorate of Overseas Surveys for the Sierra Leone Government, Series G742 (D.O.S. 419), 2nd ed. 1964–73.

Bagru River	7 43N 12 31W; 0–15 m (0–50 ft)
Bambawo – Forest School and collecting area	8 01N 11 09W; 300–460 m (1000–1500 ft)
Bo	7 58N 11 45W; 90–105 m (300–350 ft)
Freetown Peninsula	
Bathurst	8 26N 13 12W; 225–255 m (750–850 ft)
Charlotte Falls	8 25 30N 13 12W; 210 m (700 ft)
Fourah Bay College Botany Reserve	8 28 30N 13 13 30W; 180–225 m (600–750 ft)
Guma Valley	8 22N 13 12W; 270–300 m (900–1000 ft)
Havelock Plateau	8 28N 13 13 15W; 340–370 m (1100–1200 ft)
Hill Station	8 27 30N 13 15W; 210–270 m (700–900 ft)
Kongo Dam	8 25N 13 12 15W; 385–400 m (1250–1300 ft)
Leicester	8 27 30N 13 13 15W; 355–415 m (1150–1350 ft)
Leicester Peak	8 27N 13 13 30W; 595 m (1950 ft)
Lumley Cove	8 27N 13 17W; 0–15 m (0–50 ft)
Mount Aureol (Fourah Bay College)	8 28 30N 13 13 15W; 240 m (800 ft)
Mountain Torrent	8 28N 13 12 45W; 150–340 m (500–1100 ft)
Picket Hill	8 17N 13 07W; 888 m (2913 ft)
Regent	8 26N 13 13W; 270–300 m (900–1000 ft)
Sugar Loaf Gap	8 25N 13 13 30W; *c.* 550 m (1800 ft)
Sugar Loaf Mountain	8 25 15N 13 13 45W; 761 m (2497 ft)
Toke	8 18 N 13 11 30W; 0–15 m (0–50 ft)
Toke-valley three km to the north-east	8 20N 13 10 30W; 45–120 m (150–400 ft)
York	8 17N 13 11W; 15–60 m (50–200 ft)
York Pass	8 18N 13 08W; 150–270 m (500–900 ft)
Giema	8 02N 11 04W; 180m (600 ft)
Gola Hills – see Lalehun	
Gola North F.R.	7 31 to 7 45 N 10 44 to 11 04W; 150–370 m (500–1200 ft)
Jawo	7 52 N 11 08W; 120–135 m (400–450 ft)
Kabala	9 35N 11 33W; 430–490m (1400–1600 ft)
Kasewe F.R. (= Kasewe Hills F.R.)	8 19 to 8 22N 12 10 to 12 13W; 75–210 m (250–700 ft)
Koinadugu	9 32N 11 22W; 520–535 m (1700–1750 ft)
Kurubonla	9 12N 10 57W; 430 m (1400 ft)
Lake Sonfon	9 15N 11 31W; 550–565 m (1800–1850 ft)
Lalehun	7 41N 10 58W; 225–240 m (750–800 ft)
Loma Mountains and surroundings	
Bintimani (Bintumane, Loma Mansa)	9 13 30N 11 07W; 1948 m (6390 ft)
Camp 1	9 13N 11 06W; 1220 m (4000 ft)
Camp 2	9 13 15N 11 07W; 1650 m (5400 ft)
Dawule (Da-Oulen)	9 10N 11 06W; 1565 m (5140 ft)
Kongbundu Valley	9 13 30N 11 07 15W at 1520 m (5000 ft)
Seradu	9 13N 11 03W; 595–610 m (1950–2000 ft)
Sokurela	9 12N 11 04W; 625 m (2050 ft)
Masimo	8 43N 11 39W; 180–195m (600–650 ft)
Musaia	9 45N 11 34W; 340–370 m (1100–1200 ft)
Musaia Agricultural Station	9 44N 11 35W; 370 m (1200 ft)
Musaia-Gbentu road one mile north of river Mongo	9 47N 11 35W; 370 m (1200 ft)
Njala	8 06N 12 05W; 45–60 m (150–200 ft)

Ghana

Co-ordinates are taken mainly from Hall (1980).

Aburi	5 51N 0 11W; *c.* 430 m (1400 ft)
Achimota	5 37N 0 14W; *c.* 60 m (200 ft)

Afram Headwaters F.R.	7 08 to 7 15N 1 32 to 1 48W; 300–370 m (1000–1200 ft)
Agogo	6 48N 1 05W; 300–610 m (1000–2000 ft)
Aiyaola F.R.	6 06 to 6 12N 0 54 to 0 59 W
Aiyinasi A.R.S.	5 02N 2 28W; 30–60 m (100–200 ft)
Amedzofe (= Amedzope)	6 51N 0 26E; 610–760 m (2000–2500 ft)
Ankasa River F.R. (now Ankasa Game Production Reserve)	5 10 to 5 25N 2 28 to 2 44W; *c.* 60m (200 ft)
Asanta	4 54N 2 17W; 0–15 m (0–50 ft)
Asenanyo F.R. (= Asenanyo River F.R.)	6 18 to 6 35N 2 04 to 2 17W; *c.* 150 m (500 ft)
Atewa Hills F.R. (= Atewa Range F.R.)	5 58 to 6 20N 0 31 to 0 41W; 610–730 m (2000–2400 ft)
Bame	6 40N 0 21E
Begoro	6 23N 0 23W; *c.* 610 m (2000 ft)
Bia North F.R. (= Bia Tributaries North F.R.)	6 37 to 6 57N 2 57 to 3 06W
Bosuso	6 18N 0 25W
Bunso (= Bunsu)	6 17N 0 28W
Esiama	4 56N 2 21W; 0–15 m (0–50 ft)
Esukawkaw F.R.	6 18 to 6 26N 0 43 to 0 52W; 180–240 m (600–800 ft)
Kade	6 05N 0 50W; *c.* 150 m (500 ft)
Kade A.R.S.	6 08N 0 55W; *c.* 150 m (500 ft)
Kibi	6 10N 0 33W; *c.* 300 m (1000 ft)
Kpedze	6 50N 0 30E; *c.* 150 m (500 ft)
Krokosua Hills F.R.	6 19 to 6 38N 2 40 to 2 56W; 300–610 m (1000–2000 ft)
Kumasi	6 41N 1 37W; *c.* 225 m (750 ft)
Legon	5 39N 0 11W; *c.* 90 m (300 ft)
Mole Game Reserve (now Mole National Park)	9 12 to 10 11N 1 33 to 2 13W; *c.* 180 m (600 ft)
Mpraeso	6 35N 0 44W
Nsuta	5 16N 1 59W; *c.* 30 m (100 ft)
Ochi Headwaters F.R. (= Ochi Headwaters Block 1 F.R.)	5 43 to 5 44N 1 16 to 1 19W; 150–180 m (500–600 ft)
Oda	5 55N 0 59W; *c.* 120 m (400 ft)
Osenasi	5 57N 0 45W
Pampramasi	6 37N 2 57W; *c.* 150 m (500 ft)
Pra-Suhien F.R.	5 14 to 5 22N 1 22 to 1 36W; 90–120 m (300–400 ft)
Southern Scarp F.R.	6 12 to 6 45N 0 17 to 0 59W; 300–610 m (1000–2000 ft)
Subri F.R. (= Subri River F.R.)	5 08 to 5 29N 1 36 to 1 54W; 90–120 m (300–400 ft)
Tafo Cocoa Research Institute	6 13N 0 22W; *c.* 150 m (500 ft)
Tarkwa	5 18N 1 59W; 90–120 m (300–400 ft)
Todome	6 42N 0 22E
Vane	6 49N 0 25E; *c.* 460 m (1500 ft)

Index of collectors

The index contains the names of all collectors who are mentioned in the catalogue more than once, together with the country(ies) and year(s) in which they collected, and the herbaria where their specimens are preserved. We have given some additional information on those people who are not included in the biographical index of collectors compiled by Hepper & Neate (1971). EWJ denotes the private herbarium of E. W. Jones.

Arnell, S. W.	Sierra Leone, 1951. S, UPS.

Barter, C.	Sierra Leone, 1857. NY (Herb. Mitten), BM.
Boughey, A. S.	Ghana, 1953. EWJ.
Brenan, J. P. M.	Sierra Leone, 1948. EWJ.
Cummins, H. A.	Ghana, 1896. BM, G (Herb. Stephani).
Deighton, F. C.	Sierra Leone, 1934–54. BM.
Donald, L. H.	American postgraduate student of linguistics. Sierra Leone, 1966. BM.
Foote, Miss V. J.	Ghana, 1937–39. BM.
Gardner, Mrs T. S.	Sierra Leone, 1958. BM.
Gledhill, D.	Sierra Leone, 1966. BM.
Hall, J. B.	Ghana, 1959–79 (some with Jones). GC, EWJ.
Harrington, A. J.	Sierra Leone, 1966. BM, FBC (a few specimens only).
Haswell, D. R.	Sierra Leone, 1963. BM.
Høeg, O. A.	Norwegian lichenologist. Sierra Leone, 1929. BM.
Hossain, M.	Ghana, 1967–69 (some with Richards). GC, EWJ.
Irvine, F.R.	Ghana, 1935–40; Sierra Leone, 1939. BM.
Jaeger, P.	Sierra Leone, 1944–45. PC.
Jeník, J.	Ghana, 1964–7. GC, EWJ, OP.
Jones, E. W.	Ghana, Sierra Leone, 1971. EWJ, BM, GC, FBC.
Jones, T. S.	Sierra Leone, 1951. BM.
Mann, G.	Sierra Leone, 1861. NY (Herb. Mitten), BM.
Marmo, V.	Sierra Leone, 1955. BM.
Marshall, C.	British student, member of Durham University Expedition to the Kambui Hills. Sierra Leone, 1966. BM.
Morton, J. K.	Sierra Leone, 1965–66. BM, FBC.
Revell, R. J.	British school teacher. Sierra Leone, 1968. EWJ.
Richards, P. W.	Ghana, 1967–69 (some with Hossain); Sierra Leone, 1971. NMW, GC, FBC, EWJ.
Saxby, H. H.	British businessman. Ghana, 1910–11. MANCH, CGE, BM.
Sellar, P. W.	Sierra Leone, 1963. BM.
Thomas, N. W.	Sierra Leone, 1914–15. BM.
Tindall, H. D.	Sierra Leone, 1954. BM.
West-Skinn, R.	Ghana, *c.* 1957. BM.

Species

I. **ACROLEJEUNEA** (Spruce) Schiffner

1. Acrolejeunea emergens (Mitten) Stephani in Engl., *Pflanzenw. Ost-Afrikas* **C**: 65 (1895); Gradst. in *Bryophyt. Biblthca* **4**: 71 (1975), var. **emergens**

Ptychocoleus emergens (Mitten) Stephani, *Sp. hepat.* **5**: 24 (1912); E. Jones in *Trans. Br. bryol. Soc.* **2**: 406 (1954).

SIERRA LEONE. Freetown Peninsula: Mount Aureol ['Oriel'], *Arnell* 2304, 2305, 2308, 2434, 2506 (UPS, fide Gradstein, *op. cit.*); on mango near Hill Station, *Høeg* s.n.; Grafton Valley (8°24′N, 13°10′W), on small tree, *Harrington* 639. Musaia Agricultural Station, on *Uapaca togoensis, Sellar* B3. Tekaw, Veterinary Department HQ (8°51′N, 12°01′W), on large tree near the Rest House, *Harrington* 113, 115. Kabala, near the District Officer's bungalow, *Harrington* 136, *Jones* 1524a. About four km south of Kabala, on small tree in swampy valley, *Harrington* 118 p.p. Five km south of Kabala, in secondary forest, *Harrington* 125 p.p. Njala, upper part of trunk of *Nauclea diderrichii, Deighton* 5313 p.p.; on north side of trunk, especially buttresses, of *Amphimas pterocarpoides, Deighton* 5603.

GHANA. Bia North F.R., near Pampramasi, in crown of large *Entandophragma, Jones* 1411. Asenanyo F.R., in crown of *Terminalia, Jones* 1413a. Kumasi, in garden, *Irvine* 18. Pra-Suhien F.R., small tree by the Rest House, *Jones* 1348. Esukawkaw F.R., *Jeník* (Herb. Jones). Kade, bole of fallen tree in forest, *Jones* s.n. Aburi, *Jones* s.n.

A lowland species, widely distributed in tropical Africa, with a preference for isolated trees, open woodland, and the crowns of trees, and climates with a strong dry season. The absence of records from the wettest parts of Sierra Leone and Ghana is noteworthy. It is also remarkable that neither of us gathered it near Mount Aureol (Fourah Bay College), where Arnell found it frequently in 1951.

var. **confertissima** (Stephani) Gradst. in *Bryophyt. Biblthca* **4**: 76 (1975).

Ptychocoleus confertissimus (Stephani) Stephani, *Sp. hepat.* **5**: 23 (1912); E. Jones in *Trans. Br. bryol. Soc.* **2**: 405 (1954).

SIERRA LEONE. Freetown Peninsula, Leicester Peak, *c.* 520 m (1700 ft), *Jones* 1457f.

Distinguishable from var. *emergens* only by the perianth, which has four main deep plicae, sometimes with one to two subsidiary plicae, whereas the perianths of var. *emergens* have six to nine shallow subequal keels. Var. *confertissima* has hitherto been recorded only from west Cameroon and southern Nigeria, where it is locally frequent.

2. **Acrolejeunea pycnoclada** (Taylor) Schiffner in Engl. & Prantl, *Nat. Pflanzenfam.* **1** (3): 128 (1893); Gradst. in *Bryophyt. Biblthca* **4**: 108 (1975).

GHANA. Aiyaola F.R. near Kade, in crown of large *Piptadeniastrum, Jones* 1232, det. Gradstein.

A species which is widely distributed in the Indo-Malayan region and Oceania, and apparently also in Madagascar, but known from continental Africa only from this collection and a single collection at Stanleyville (now Kisangani), Zaire. Gradstein (*op. cit.*) states that 'the species grows preferably in anthropogenic habitats'; the occurrence in the Aiyaola F.R. does not show this preference, but suggests rather that *Acrolejeunea pycnoclada* is a component of the 'tree crown flora'.

II. **ANEURA** Dumort.

1. **Aneura pinguis** (L.) Dumort., *Syll. Jungerm. Europ.*: 86 (1831).

Riccardia pinguis (L.) Gray, *Nat. arr. Brit. pl.* **1**: 684 (1821); E. Jones in *Trans. Br. bryol. Soc.* **3**: 84 (1956).

SIERRA LEONE. Kambui Hills, Bambawo, on damp silt in floor of old mine workings, *Jones* 1542.
GHANA. Pra-Suhien F.R., on rotting logs, *Jones*!

III. **ANTHOCEROS** L.

1. **Anthoceros buettneri** Stephani, *Sp. hepat.* **5**: 997 (1916).

GHANA. Legon Botanical Garden, *Hall* (GC 47098).

Agrees well with the isotype from Bismarkburg, Togo (FH); the holotype (G) is too fragmentary to be useful. It is a small plant with the habit of *Anthoceros crispulus* auct., but differing in the spores, which are black, 40–45μm diam., and densely clothed on all faces with spines 1–2 μm long.

2. **Anthoceros mandonii** Stephani, *Sp. hepat.* **5**: 997 (1916); Vanden Berghen in *Résult. scient. Explor. hydrobiol. Bassin Lac Bangweolo & Luapula* **8**(1): 195 (1972); *Bull. Jard. bot. natn. Belg.* **48**: 371 (1978).

SIERRA LEONE. Loma Mountains, Bintimani, 1830–1940 m (6000–6360 ft), on soil over rocks, west-facing cliffs. *Harrington* 212 p.p. and summit plateau, *Morton* s.n.

Anthoceros spp. are certainly more widespread than the above records indicate; we have seen plants which cannot be named specifically from Amedzofe and elsewhere in Ghana.

IV. **ARACHNIOPSIS** Spruce

1. **Arachniopsis diacantha** (Montagne) M. Howe in *Bull. Torrey bot. Club* **29**: 288 (1902).

SIERRA LEONE. Loma Mountains: on bole of large tree in forest near 'Camp 2', 1650 m (5400 ft), *Jones* 1482; on moist bank of streamlet in deep shade, *c.* 1520 m (5000 ft), *Jones* 1496 p.p. Kambui Hills, Bambawo, in forest on plateau, on charred stump, *Jones* 1546 p.p. Gola North F.R., rotten log by stream in forest, *Jones* 1566b.

GHANA. Ankasa River F.R., on rotting log, *Jones* 1366 p.p.; on rotting bark in swampy forest one mile south of the Ankasa River, *Richards* R7061 p.p. Aiyinasi A.R.S., on rotting log in forest, *Jones* 1361a, 1362. Subri F.R., *Jones* ! Pra-Suhien F.R., on rotting log, *Jones* 1335. Amedzofe, near the waterfall, *Irvine* 411.

Widely distributed throughout the forest of the wettest parts of W. Africa, usually on rotting logs, but occasionally on earth or tree boles, and associated (as in all the above records except *Jones* 1482) with *Lophocolea martiana* subsp. *newtonii* (Stephani) R. M. Schuster; *Cephalozia fissa* Stephani is also a frequent associate.

Fulford (1968) followed earlier authors in recognizing two allied species in S. America: *Arachniopsis diacantha* with stiff leaf segments 5–8 cells long, the cells mostly 130 μm long, and *A. coactilis* Spruce with flaccid leaf segments 6–8–(10) cells long, the cells 78–90 μm long. African plants are intermediate in one respect or another between these two, though they tend to be nearer to *A. diacantha.* We follow Arnell (1963) in considering the two species to be synonymous.

V. **ARCHILEJEUNEA** (Spruce) Schiffner

1. **Archilejeunea abbreviata** (Mitten) Vanden Berghen in *Revue bryol. lichén.* **20**: 117 (1951).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., on bole of isolated tree near Heddle's Farm, *Jones* s.n.; Leicester Peak, on mango, *Jones* 1464a; near Toke, on shaded boulder by stream, *Jones* 1448, and on branches of isolated shrub nearby, *Jones* s.n. Lake Sonfon, on low tree in forest surrounding the 'lake', *Harrington* 40 p.p. Bagru ['Bagroo'] River, *Mann* s.n. (*Lejeunea abbreviata* Mitten – NY, holotype; BM, isotype).

GHANA. Krokosua Hills, 460 m (1500 ft), on liane, *Jones* 1389. Asenanyo F.R., on buttress of large tree and on pole-size tree boles by the river, *Jones* 1413b, c. Subri F.R., on bole of large tree in *Raphia* swamp, *Jones* 1358. Bunso, on cocoa, *Jones* 1317a p.p. Bunso–Begoro road, on liane by stream, *Jones* 1302a. Southern Scarp F.R., near Begoro, on small pole, *Jones* 1306. Kade, on small tree in deep shade, *Jones* s.n. Amedzofe, in old coffee farm, *Jones* 1249; on log near the waterfall, *Jones* 1282.

See note following *Archilejeunea autoica.*

2. **Archilejeunea africana** Stephani, *Sp. hepat.* **4**: 705 (1911); Vanden Berghen in *Revue bryol. lichén.* **20**: 114 (1951).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., epiphyllous, *Jones* s.n.; Regent, tree in farm bush, *Harrington* 409 p.p.; York Pass, on twigs of sapling in forest understorey, *Harrington* 631, 637a, 638. Masimo, *Marmo* 161 p.p. Kasewe F.R., on twig in rocky stream bed in forest, *c.* 90 m (300 ft), *Richards* R7165b, and epiphyllous, *Richards* R7170 p.p., both det. Jones. Njala, upper part of trunk of *Nauclea diderrichii, Deighton* 5313 p.p. Kambui Hills, Bambawo, on small trees in forest near the Rest House, *Jones* 1527, 1532b. Giema, epiphyllous in secondary forest near stream, *Harrington* 528 p.p.. 529 p.p. Gola Hills: Gola North F.R., in primary forest, epiphyllous, *Jones* 1568 p.p., and on twigs of understorey 'shrublets', *Jones* 1569 p.p.; near Lalehun, epiphyllous, *Marshall* s.n.

GHANA. Pampramasi, on small pole in damp forest, *Jones* 1408c. Aiyinasi, in forest, on buttress of *Uapaca, Jones* 1361d. Nsuta, on liane in secondary forest on bank of Pra river, *Jones* 1351b. Southern Scarp F.R., near Begoro, on small pole, *Jones* 1306b.

See note following *Archilejeunea autoica.*

3. **Archilejeunea autoica** Vanden Berghen in *Revue bryol. lichén.* **20**: 119 (1951).

SIERRA LEONE. Kambui Hills, forest on plateau above Bambawo, *Jones* 1544.

GHANA. Pampramasi, rotting log by stream in forest, *Jones* 1410b, on rocks in the stream bed, 1410c, and tree root in the bank, 1410d. Krokosua Hills F.R., on small poles and lianes in understorey, *c.* 460 m (1500 ft), *Jones* 1391, 1392b. Pra-Suhien F.R., side of tree root, *Jones* 1343b. Kade, base of liane in forest in deep shade, *Jones* 1219.

Archilejeunea abbreviata, A. africana, and *A. autoica* are closely allied; indeed Vanden Berghen (1972: 90) has suggested that the first two are synonymous. Nevertheless I have rarely had difficulty in separating them. *A. africana* often seems distinct in its habit, with closely-spaced long-beaked perianths ranked along one side of the branches of a cyme. In contrast *A. abbreviata* is more irregularly branched, with the subgynoecial innovations not again quickly fertile, and the perianths usually less cordate and with short beaks. Moreover, the two species often grow in different places, with *A. abbreviata* showing a preference for less-sheltered habitats. In *Jones* 1306 the two species were noted in the field as growing close together on the same branches, but quite distinct, *A. africana* being green when fresh, and *A. abbreviata* being brown. [E.W.J.]

On the other hand I find great difficulty in separating *Archilejeunea autoica* from *A. abbreviata*. Intermediates are frequent (some of the specimens listed above are intermediate), and *A. autoica* is almost always associated with *A. abbreviata* (e.g. in the Krokosua Hills, *Jones* 1389 and 1391, and at Kade, *Jones* s.n. and 1219) under conditions that suggest that *A. autoica* is merely a modification of *A. abbreviata* induced by deep shade or moisture. [E.W.J.]

The frequency with which *A. africana* (but not *A. abbreviata*) occurs as an epiphyllous hepatic in Sierra Leone is remarkable; I have not recorded it as such elsewhere. [E.W.J.]

4. **Archilejeunea linguaefolia** Stephani, *Sp. hepat.* **4**: 708 (1911); Vanden Berghen in *Revue bryol. lichén.* **20**: 113 (1951).

SIERRA LEONE. Musaia Agricultural Station, pumping station, epiphyte, *Haswell* B1 p.p. Kenema, on the banks of the Moa river at Jawo, on tree boles, roots and branches, and on banks of sand in the flood zone, 'usually the only bryophyte present, and in great quantity from near present water level throughout the flood zone' (field note), *Jones* 1537. Gola Hills, Lalehun, on boulders in dry stream bed in forest, *Jones* 1553.

VI. ASTERELLA P. Beauv.

1. **Asterella abyssinica** (Gottsche) Grolle ex Vanden Berghen in *Résult. scient. Explor. hydrobiol. Bassin Lac Bangweolo & Luapula* **8** (1): 170 (1972).

Fimbriaria abyssinica Gottsche, *Syn. hepat.*: 569 (1846).

SIERRA LEONE. Loma Mountains, Bintimani, cliffs near the summit, in crevices, *Jones* 1486, det. Grolle.

Asterella abyssinica is frequent on Mont Cameroun (Cameroon Mountain) at similar altitudes (*Jones* 330, 433, 434).

VII. BAZZANIA Gray

1. **Bazzania decrescens** (Lehm. & Lindenb.) Trev. St. Léon in *Memorie Ist. lomb. Sci. Lett.* **13**: 414 (1877), subsp. **molleri** (Stephani) E. Jones in *J. Bryol.* **8**: 303 (1975).

SIERRA LEONE. Loma Mountains: 1220–1680 m (4000–5500 ft), frequent on the boles of large *Parinari* etc. on the margins of the forest, *Jones* 1478b, 1489, 1507; *Harrington* 334 p.p., 336 p.p.

GHANA. Ankasa River F.R., on tree boles near the ground, *Jones* 1372a, b. Atewa Hills F.R., in swamp forest on boles of large *Lophira, Jones* 1328 p.p. 1331 p.p.; on bole of *Gilbertiodendron limba,* 790 m (2600 ft), *Richards & Hossain* (GC36670).

For a discussion of the variability of this plant see Jones (*op. cit*). It is widely distributed but local in Africa, and is usually abundant where it occurs. It is usually montane; its occurrence in the Ankasa River F.R. is remarkable, and the fact that it was growing close to the river, some of it (*Jones* 1372b) in a site where it may possibly be irrigated in periods of high water, may indicate that high rainfall is usually a factor that controls its distribution.

VIII. BRACHIOLEJEUNEA (Spruce) Schiffner

1. **Brachiolejeunea tristis** Stephani, *Sp. hepat.* **5**: 112 (1912); Vanden Berghen in *Bull. Soc. r. Bot. Belg.* **92**: 115 (1960).

Brachiolejeunea camerunensis E. Jones & Vanden Berghen in *Bull. Jard. bot. État Brux.* **21**: 88 (1951).

SIERRA LEONE. Loma Mountains, on branches of isolated trees in rocky ground etc. near 'Camp 2', 1680 m (5500 ft), mixed with *Marchesinia moelleriana, Lopholejeunea jonesii, Frullania* spp. etc., *Jones* 1480 p.p., 1495 p.p.

This species is widely distributed in the African mountains but is unlikely to occur elsewhere in Sierra Leone unless in the Tingi Hills, or in Ghana.

IX. CALYPOGEIA Raddi

1. **Calypogeia fissa** (L.) Raddi, *Jungermanniografia Etrusca*: 33 (1818); Bischler in *Revue bryol. lichén.* **37**: 97 (1970).

SIERRA LEONE. Loma Mountains, moist bank of streamlet in deep shade, *c.* 1520 m (5000 ft), *Jones* 1496 p.p.

Oil bodies have not been seen, but the plant when fresh lacked any blue tinge, and it agrees well with African plants accepted as *Calypogeia fissa* by Bischler (*op. cit.*), and with plants from Tanzania (*Jones* 1959, 1964) referred to by Jones (1976: 44).

2. **Calypogeia longifolia** Stephani, *Sp. hepat.* **6**: 449 (1924); Bischler in *Revue bryol. lichén.* **37**: 106 (1970).

SIERRA LEONE. Loma Mountains, head of the Kongbundu Valley, north-west of Bintimani, *c.* 1520 m (5000 ft), on vertical banks of moist humic earth in grassland, *Jones* 1502 p.p.

Bischler (*op. cit.*) gives the distribution of this species as South Africa (Cape Province, Natal, Transvaal), Lesotho, Swaziland, Southern Rhodesia (= Zimbabwe), and central Madagascar.

X. CAUDALEJEUNEA (Stephani) Schiffner

1. **Caudalejeunea africana** (Stephani) Schiffner in Engl. & Prantl, *Nat. Pflanzenfam.* **1** (3): 129 (1893); Vanden Berghen in *Revue bryol. lichén.* **17**: 96 (1948).

GHANA. Ankasa River F.R., epiphyllous in crown of *Glutea, Jones* 1378c; on palm in swamp one mile south of the Ankasa bridge, *Jones* 1382 p.p. Subri F.R., on fronds of *Raphia* in swamp forest, *Jones* 1355.

A very local species, which is probably confined to the lowland rain forest of West Africa and the Congo Basin; usually, as in the three Ghana records, epiphyllous, though by no means exclusively so.

2. **Caudalejeunea dusenii** Stephani, *Sp. hepat.* **5**: 11 (1912); E. Jones in *Trans. Br. bryol. Soc.* **2**: 165 (1953).

GHANA. Aiyinasi A.R.S., boughs of a small tree by the Rest House, *Jones* 1384a. Aiyaola F.R., near Kade A.R.S., on twigs and small branches in the crown of a *Piptadeniastrum, Jones* 1236 p.p., and of *Khaya, Jones* 1237b. Amedzofe, on cocoa trees, *Jones* 1272c.

Caudalejeunea dusenii usually grows in rather open well-illuminated places on small branches and twigs, thus in the crowns of large forest trees, but also on bushes and small trees of farms and gardens. It has been recorded from Nigeria (Jones, *op. cit.*), Cameroon (Jones, *op. cit.*; Augier, 1974) and, more recently, from the Uluguru Mountains in Tanzania (Bizot & Pócs, 1979).

3. **Caudalejeunea hanningtonii** (Mitten) Schiffner in Engl. & Prantl, *Nat. Pflanzenfam.* **1** (3): 129 (1893); Vanden Berghen in *Revue bryol. lichén.* **17**: 98 (1948).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., frequent both as an epiphyll and on twigs, *Harrington* 78 p.p., 80, 82 p.p., *Jones* 1440b and s.n.; Leicester Peak, on old mango, *Jones* 1464 p.p. Kafogo ['Kafoko'] (9°24'N, 11°44'W), 240 m (800 ft), *Thomas* 2126a. Loma Mountains, forest above Seradu, 1040 m (3400 ft), epiphyllous, *Jones* s.n. Kasewe F.R., on twig in rocky stream bed in forest, *c.* 90 m (300 ft), *Richards* R7165a, and epiphyllous, *Richards* R7170 p.p. Giema, on low vegetation by stream in secondary forest, *Harrington* 529 p.p., 532 p.p.

GHANA. Krokosua Hills, on cocoa, *Jones* 1388. Aiyinasi, on *Uapaca* bole in forest near the A.R.S., *Jones* 1361e; epiphyllous near the river Fiakpole, *Jones* 1364b. Pra-Suhien F.R., epiphyllous, *Jones* 1345b. Bunso, on cocoa, *Jones* 1317b; near the Bosuso–Begoro road, on liane, *Jones* 1302c. Forest near Kade A.R.S., epiphyllous, *Jones* s.n. Osenasi (16 km south-east of Kade), on cocoa, *Jones* s.n. Aburi Botanical Gardens, *Jones* s.n. (GC). Kpedze, on cocoa, *Jones* s.n.

Much the most widespread and commonest species of *Caudalejeunea* in tropical Africa. It is generally distributed throughout southern Ghana, especially on small trees such as cocoa in farms, and on bushes and small trees in secondary forest, usually on tree branches, though occasionally epiphyllous; this agrees with Jones' experience of it in most other parts of Africa. It is curious that in Sierra Leone almost all the records show it as being epiphyllous. It is not clear whether this indicates a genuine difference in habitat-preference, which might be due to the climatic peculiarities of the country, or whether it is merely due to the lack of collecting in the farmland and secondary forest of central and southern Sierra Leone.

4. Caudalejeunea tricarinata E. Jones in *Trans. Br. bryol. Soc.* **2**: 169 (1953).

SIERRA LEONE. Freetown Peninsula: three km north-east of Toke, on branch of a small isolated shrub growing amongst rock slabs, *Jones* 1448c; York Pass, epiphyllous, *Harrington* 626 p.p. Kasewe F.R., on savanna tree, *Richards* s.n. (Herb. Jones). Njala, upper part of trunk of 66 foot-tall *Nauclea diderrichii*, *Deighton* 5313 p.p.

Hitherto known only from Nigeria (Jones *op. cit.*, 1968*b*) and Cameroon (Augier, 1978).

Schuster (1980) finds 'no reliable differences' to separate *Caudalejeunea tricarinata* from the polymorphic American species, *C. lehmanniana* (Gottsche) A. W. Evans. Accordingly he reduces the name to a synonym of *C. lehmanniana.*

XI. CEPHALOZIA (Dumort.) Dumort.

1. Cephalozia fissa Stephani in *Hedwigia* **30**: 204 (1891).

GHANA. Ankasa River F.R., on rotting log, *Jones* 1366. Aiyinasi A.R.S., in forest, *Jones* 1361a. Tarkwa, *Saxby* s.n.

A lowland species, widely distributed in rain forest in tropical Africa on rotting wood, where it is often associated with *Arachniopsis.* It is likely to be present in south-eastern Sierra Leone.

XII. CEPHALOZIELLA (Spruce) Schiffner

1. Cephaloziella ?vaginans Stephani in *Wiss. Ergebn. dt. ZentAfr. Exped.* **2**: 119 (1911).

SIERRA LEONE. Loma Mountains, valley west of Bintimani, *c.* 1650 m (5400 ft), on bole of large tree on forest margin, *Jones* 1493, det. Váňa.

Hitherto known from Ruwenzori (G, type), Kilimanjaro (*Jones* 2246, det. Váňa, BM and Herb. Jones) and, as var. *camerunensis* S. Arnell (Arnell, 1958), from Mont Cameroun (Cameroon Mountain).

XIII. CERATOLEJEUNEA (Spruce) Schiffner

1. Ceratolejeunea beninensis E. Jones & Vanden Berghen in *Bull. Jard. bot. État Brux.* **21**: 63 (1951).

GHANA. Ankasa River F.R., on leaves of low shrubs in small gaps in forest by the river, mixed with *Ceratolejeunea diversicornua, Cololejeunea cornuta, Trachylejeunea serrulata* etc., *Jones* 1375 p.p.

Ceratolejeunea beninensis was previously known only from Benin, Nigeria, and Cameroon (Banga F.R., *Jones* 284). Perianths are uncommon.

2. Ceratolejeunea calabariensis Stephani in *Hedwigia* **34**: 234 (1895); Vanden Berghen in *Bull. Jard. bot. État Brux.* **21**: 71 (1951); *Revue bryol. lichén.* **39**: 381 (1973).

Ceratolejeunea saxbyi Pearson in *Mem. Proc. Manchr lit. phil. Soc.* **65** (1): 4 (1921).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., on trees, *Harrington* 579, 580, 666 p.p., *Jones* 1420; Sugar Loaf, 460 m (1500 ft), *T. S. Jones* 245 p.p. Bagru ['Bagroo'] River, mixed with *Thysananthus spathulistipus, Mann* s.n. Kambui Hills, Bambawo, on large roadside trees, *Harrington* 569 p.p., 570 p.p.; *Jones* 1550a; on smooth bole of small tree in forest, *Jones* 1530; on earth bank by road in forest, *Jones* 1529. Gola Hills: Lalehun, upper part of bole of large tree, *Jones* 1554b p.p.; buttress of *Piptadeniastrum, Jones* 1555b; Gola North F.R., on boughs in crown of large tree, mixed with *Marchesinia excavata, Jones* 1562.

GHANA. Tarkwa, *Saxby* (MANCH, holotype of *Ceratolejeunea saxbyi*; BM, isotype), and mixed with *Taxilejeunea nicholsonii* Pearson, *Saxby* (CGE). Pra-Suhien F.R., on mango by the Rest House, *Jones* 1349. Atewa Hills F.R., on trunk of *Cassipourea, Richards & Hossain* (GC 36668 p.p.); boughs in crowns of *Cassipourea, Jones* 1297, 1322 p.p. Kade A.R.S., mixed with *Cheilolejeunea trifaria* on main bough of *Parinari glabra* in forest, *Hossain* (GC 36696).

The problems concerning the delimitation and taxonomy of *Ceratolejeunea calabariensis* are discussed under *C. zenkeri*. Of the plants recorded above that have been examined by Jones, 1554b, 1349 and *C. saxbyi* have perianth horns 100–150 μm long, and would thus be *C. calabariensis* as defined by Vanden Berghen in 1951, while the remainder have longer horns, mostly 200–300 μm long. The plants from the Atewa Hills have perianth horns up to 350 μm or exceptionally 400 μm long, and might be considered intermediate to *C. zenkeri*.

3. Ceratolejeunea diversicornua Stephani, *Sp. hepat.* **5**: 410 (1913); Vanden Berghen in *Bull. Jard. bot. État Brux.* **21**: 68 (1951); *Bull. Jard. bot. natn. Belg.* **47**: 206 (1977).

GHANA. Ankasa River F.R., on leaves of shrubs with *Ceratolejeunea beninensis, Jones* 1375 p.p., det. Vanden Berghen; *Jeník* s.n. (OP); on palm leaves in swamp one mile south of the Ankasa bridge, *Jones* 1382 p.p.

Ceratolejeunea diversicornua is a rare species otherwise known only from Cameroon and Kivu. In many respects the Ankasa River plants are intermediate between *C. diversicornua* and *C. cornutissima* Stephani as described by Vanden Berghen (1951), thus supporting his later (1977) suggestion that the two species may be synonymous. The sterile shoots differ from those of *C. beninensis,* when the two species are mixed, in bearing utricles and in having leaves which are less falcate with margins distantly serrulate (as illustrated by Vanden Berghen (1951: fig. 23F) for *C. cornutissima*) due to slightly projecting radial walls. The perianth horns are only *c.* 200 μm long; shorter than described by Vanden Berghen (1951).

4. Ceratolejeunea zenkeri Stephani, *Sp. hepat.* **5**: 449 (1913), sensu Vanden Berghen in *Bull. Jard. bot. État Brux.* **21**: 78 (1951).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., on stones, *Harrington* 605, on *Dacryodes klaineana, Harrington* 586, on large tree, *Harrington* 666 p.p., epiphyllous, *Jones,* s.n.; Leicester Peak, on tree bole, *Brenan* (*Jones* 461, det. Vanden Berghen), on bough of *Combretum, Jones* 1454 p.p. Giema, on sapling, *Harrington* 554 p.p.

GHANA. Krokosua Hills F.R., tree boles on sheltered woodland margin, 550 m (1800 ft), *Jones* 1406. Ankasa River F.R., in crown of *Glutea, Jones* 1378a. Pra-Suhien F.R., bough in crown of tree, *Jones* 1346.

Vanden Berghen (1951) recognized three closely allied species (and also other more distinct species) in Africa (excluding the Mascarenes), for which he used the names *Ceratolejeunea calabariensis* Stephani, *C. jungneri* Stephani, and *C. zenkeri* Stephani. They were said to differ chiefly in the lengths of the perianth horns, which were 100–150 μm, 200–280 (exceptionally 360) μm, and 330 (exceptionally as short as 280)–530 μm respectively. In addition *C. zenkeri* differed from the other two in having ocelli which, in many leaves, formed a conspicuous vitta extending to near the middle of the leaf. Vanden Berghen pointed out that the vegetative differences between *C. calabariensis* and *C. jungneri* were slight, and in 1973, influenced by the variability in length of horn that he observed in certain collections, he made them synonymous under the name *C. calabariensis.* Specimens with horns about 300 μm long, thus in the range of overlap between '*C. jungneri*' and '*C. zenkeri*' are common (12 of the 40 specimens in Herb. Jones under the preceding three names), and these may or may not have a vitta. The vitta thus becomes the chief distinguishing feature of *C. zenkeri.* A vitta is, however, often present in some leaves but not in others; in *Jones* 1346, for example, it is present in branch leaves but not in stem leaves. The different forms often occur in association with each other, and sometimes indeed intimately mixed, but it is not clear whether such mixtures consist of different genotypes or are the result of intraclonal variation. Thus there are strong reasons for merging *C. zenkeri* with *C. calabariensis*. Nevertheless the variation within the taxon that would be so formed is so great that some division seems desirable; moreover a reasonably large proportion of collections are homogeneous. We have therefore tentatively continued to recognize two taxa, *C. calabariensis* and *C. zenkeri*, and retained the names used by Vanden Berghen, even though these names are almost certainly not correct.

Ceratolejeunea calabariensis is probably identical with the earlier *C. belangeriana* (Gottsche) Stephani from Mauritius. *C. belangeriana* itself is, however, almost certainly identical with one or more of the still earlier species from the West Indies and Central and South America – *C. cornuta* (Lindenb.) Schiffner, *C. maritima* (Spruce) Stephani, and *C. variabilis* (Lindenb.) Schiffner. Examination of the literature and of herbarium specimens shows that there is great confusion between these plants, and it will not be possible to decide the correct name for *C. belangeriana* until the American members of the complex have been more closely studied. We therefore retain a late name, *C. calabariensis,* the application of which is certain, rather than adopt an earlier name, the application and correctness of which are doubtful.

Vanden Berghen (1951) used the name *Ceratolejeunea zenkeri* for plants with a vitta and long-horned perianths with considerable hesitation, his justification being that part of the collection *Zenker* 3935g preserved in the BM possesses these features. The only specimen labelled *C. zenkeri* in Stephani's own herbarium is a portion of *Zenker* 3935g, but is *C. calabariensis*. Moreover Stephani's 'Icones' show *C. zenkeri* as a short-horned plant, while his original descriptions are too lax to differentiate between *C. zenkeri* sensu Vanden Berghen and *C. calabariensis. Zenker* 3935g was a large collection, as the portion in the BM shows, and it doubtless included both taxa.

XIV. **CHANDONANTHUS** Mitten

1. Chandonanthus hirtellus (Fried. Weber) Mitten in *J. Linn. Soc.* (Bot.) **22**: 321 (1886); Vanden Berghen in *Bull. Soc. r. Bot. Belg.* **98**: 137 (1965).

SIERRA LEONE. Loma Mountains, 1650 m (5400 ft), on the boles of large *Parinari* on the forest margin, *Jones* 1478a, 1493.

A species with a wide but disjunct distribution, chiefly in the mountains of Africa and the Old World tropics. On the Loma Mountains it occurs in a wide range of forms, from robust shoots with four-lobed leaves down to slender *Lophozia*-like plants with bilobed leaves, creeping amongst *Bazzania decrescens* subsp. *molleri, Conoscyphus trapezioides,* and various Lejeuneaceae.

XV. **CHEILOLEJEUNEA** (Spruce) Schiffner

1. Cheilolejeunea decursiva (Sande Lacoste) R. M. Schuster in *Beih. nov. Hedwigia* **9**: 112 (1963); Grolle in *J. Bryol.* **9**: 531 (1977).

Cheilolejeunea tisserantii Vanden Berghen & Jovet-Ast in *Revue bryol. lichén.* **20**: 105 (1951).

SIERRA LEONE. Freetown Peninsula: by Mountain Torrent below Havelock Plateau, on base of small tree, mixed very sparsely with other small Lejeuneaceae, *Jones* 1441b, and on *Vitex, Jones* 1443; three km north-east of Toke, *c.* 90 m (300 ft), on bole of small tree growing in rock pavement, *Jones* 1448b. Loma Mountains: epiphyllous in gallery forest *c.* one km west of 'Camp 2', 1520 m (5000 ft), *Morton* (*Harrington* 347 p.p.); 1680 m (5500 ft), *Jones* 1483a p.p.

There are very few records of this species from Africa, though it is evidently widely distributed, as it is known from Réunion, Madagascar, Tanzania, Zaire, the Central African Republic, and

Guinea. It would be difficult to detect if it were to be present, as it is in *Jones* 1441b, in small amounts mixed with common species, such as *Lejeunea caespitosa* and *L. eckloniana,* so that it has probably been overlooked.

2. Cheilolejeunea exinnovata E. Jones in *J. Bryol.* **12**: 37 (1982).

SIERRA LEONE. Gola North F.R., in unexploited forest, epiphyllous, *Jones* 1568 p.p. (BM, holotype).

GHANA. Ankasa River F.R., epiphyllous on shrublets in small gap near the river, *Jones* 1375 p.p.

The species is also known from Zimbabwe, and is present in Spruce's L419 from São Gabriel, Brazil (MANCH, sub *Cheilolejeunea aneogyna*).

3. Cheilolejeunea intertexta (Lindenb.) Stephani in *Bull. Herb. Boissier* **5**: 79 (1897); Grolle in *J. Hattori bot. Lab.* **46**: 344 (1979).

Cheilolejeunea inflata Stephani, *Sp. hepat.* **5**: 645 (1914); E. Jones in *Trans. Br. bryol. Soc.* **2**: 385 (1954).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., epiphyllous, *Harrington* 78 p.p., 82 p.p., 84, 87 p.p., and on bark, *Harrington* 586 p.p., 596 p.p.; Mountain Torrent, below Havelock Plateau, on *Vitex, Jones* 1443 p.p.; Leicester Peak, 550 m (1800 ft), *Jones* s.n.; valley three km north-east of Toke, on isolated shrub, *Jones* s.n.; Black Johnson Beach near York, epiphyllous on low shrub in thicket behind the beach, *Harrington* s.n. Kambui Hills, Bambawo, on tree boles in forest, *Jones* 1527 p.p., 1532d, 1533. Giema, on sapling by road, *Harrington* 554 p.p.

GHANA. Bia North F.R., in crown of *Entandophragma, Jones* 1411c. Ankasa River F.R., *Richards* (GC 36679). Aiyinasi A.R.S., on *Citrus, Jones* 1383c. In scrub near Esiama, *Jones* 1365. Pra-Suhien F.R., trees by the Rest House, *Jones* 1350a. Bunso, on cocoa, *Jones* 1317a. Between Bame and Todome, on cocoa, *Jones* s.n.

See notes under *Cheilolejeunea serpentina.*

4. Cheilolejeunea newtonii Stephani ex Schiffner in Engl. & Prantl, *Nat. Pflanzenfam.* **1** (3): 124 (1893); E. Jones in *Trans. Br. bryol. Soc.* **2**: 388 (1954).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., on tree boles, *Jones* 1419a, b, *Harrington* 582, on rock, *Jones* 1422; Havelock Plateau, *Jones* s.n.; Leicester Peak, on tree bole, *Jones* 1430a, on rock, *Jones* 1452a; Regent, *Irvine* 204b, 205, 231; Bathurst, Kongo Dam, on boulder, *Jones* 1435; Dighton Dam. No. 1, valley below Sugar Loaf, on boulder, *Harrington* 661 p.p.; three km north-east of Toke, on shaded boulder, *Jones* 1447. Kambui Hills, Bambawo, shady earth bank by road, *Jones* 1529. Gola North F.R., on buttress of tree, *Jones* s.n. Banks of the Moa river at Jawo, on tree bole at top of flood zone, *Jones* 1538b.

GHANA. Ankasa River F.R., on bole of *Parinari, Richards* (GC36679 p.p.), epiphyllous, *Jones* 1375 p.p. Tarkwa, *Saxby* (CGE). Esukawkaw F.R., *Jeník.* Kade A.R.S., on old lianes in forest in deep shade, *Jones* 1217 p.p. (GC). Amedzofe, 760 m (2500 ft), on decaying tussocks of *Catagyna* (= *Afrotrilepis*), *Jones* 1253, and on shaded rocks, *Jones* 1255.

Cheilolejeunea newtonii is known only from West Africa; it seems to be exceptionally abundant on the Freetown Peninsula, where it is probably the commonest species of *Cheilolejeunea.* It resembles *C. intertexta*, with which it often grows, in being monoecious. Well-developed plants differ in being somewhat larger (strong shoots of *C. intertexta c.* 0·9 mm wide, of *C. newtonii* 1·0–1·2 mm wide), with the keels of the lobule making a more distinct narrower sinus with the postical margin of the lobe (in *C. intertexta* the keel is almost in line with the postical margin of lobe), but weak shoots of *C. newtonii* may be indistinguishable from *C. intertexta* vegetatively. Thus mixtures of the two species, which are not infrequent, are very confusing, and it was such mixtures that led Jones (1973) to conclude that the two species were synonymous. Grolle (1979), however, pointed out that in *C. intertexta* the first leaf to be formed on a subgynoecial innovation is an underleaf, while in *C. newtonii* the first leaf is a lateral leaf. This order is not absolutely constant, however; though there is a great preponderance of the one type of innovation in any plant, as many as one in ten innovations may be of the other kind. Occasionally when twin subgynoecial innovations have been formed, one member of the pair has an underleaf first, while its companion has a lateral leaf first.

Cheilolejeunea newtonii is probably more restricted to areas of high rainfall than either *C. intertexta* or *C. serpentina*.

5. **Cheilolejeunea serpentina** (Mitten) Mizutani in *J. Hattori bot. Lab.* **26**: 171 (1963); Grolle in *J. Hattori bot. lab.* **46**: 346 (1979).

Cheilolejeunea principensis Stephani ex Paris in *Revue bryol.* **33**: 38 (1906); E. Jones in *Trans. Br. bryol. Soc.* **2**: 383 (1954).

SIERRA LEONE. Freetown Peninsula: Mount Aureol ['Oriel'], *Arnell* 2507; Fourah Bay College B.R., on tree boles, *Jones* 1420 p.p., on liane, *Harrington* 596 p.p.; Leicester Peak, *Brenan* (*Jones* 464 p.p., 476 p.p.); Lumley Cove, tree bole on the beach, *Richards* (*Jones* 467); Regent, small tree in farm bush, *Harrington* 408 p.p.; Sugar Loaf Mtn, *Tindall* 62 p.p.; valley three km north-east of Toke, *Jones* s.n.; Toke, on small trees in 'coastal savanna' behind the beach, *Jones* 1444c, 1446b. Musaia Agricultural Station, pumping station, *Haswell* Bl p.p. Lake Sonfon, on *Erythrophleum* on edge of forest surrounding the 'lake', *Harrington* 53 p.p. Between Sokurela and Kurubonla, on *Uapaca, Jones* 1522d. Njala, upper part of trunk of *Nauclea diderrichii, Deighton* 5313 p.p. Kambui Hills, Bambawo, on mango, *Harrington* 427 p.p., 437 p.p., on roadside tree, *Harrington* 569 p.p., 570 p.p. Giema, on fallen tree in secondary forest, *Harrington* 536 p.p. Lalehun, upper part of bole of large tree, *Jones* 1554 p.p. Gola North F.R., in crown of large tree, *Jones* 1560 p.p.

GHANA. Ankasa River F.R., on *Pentadesma* bole, *Richards* (GC 36674, 36678), epiphyllous, *Jones* 1375 and *Jeník* s.n. Aiyinasi A.R.S., on *Citrus, Jones* 1383a. Pra-Suhien F.R., bough of tree by the Rest House, *Jones* 1350a p.p. Aiyaola F.R. near Kade, in crown of *Piptadeniastrum*, *Jones* 1232b. Osenasi, on cocoa, *Jones* s.n. Aburi Botanical Gardens, *Irvine* s.n. Amedzofe, *Irvine* 412; on *Terminalia* and *Lophira* near top of hill, *Jones* 1257e.

Cheilolejeunea serpentina differs from *C. intertexta* and *C. newtonii* in being dioecious and in having a rounder leaf with a more strongly arched keel; the first leaf on a subgynoecial innovation is a lateral leaf (as in *C. newtonii*). *C. serpentina* and *C. intertexta* are the two commonest species of the genus throughout much of West Africa, where indeed they are amongst the most abundant schizostipulean Lejeuneaceae. They also occur in East Africa where, however, they are very local, as they are essentially lowland species and confined to limited areas of high humidity, chiefly near the coast. The two species often grow mixed, and appear to be more tolerant of drought and exposure than most other schizostipulean Lejeuneaceae; thus they often occur in the crowns of large trees, and on the small branches and twigs of isolated bushes. Usually they grow on bark or on rock, but in districts with very high rainfall, such as the Freetown Peninsula and the Ankasa River F.R., they are epiphyllous. *C. serpentina* is often abundant on the seacoast, where it may occur (as at Toke) very close to the high-water-mark, and clearly must tolerate some salt. *C. newtonii* is certainly much more restricted in range, probably by a lower tolerance of drought, and in most districts is much less abundant, though it grows in similar habitats, and is often mixed with one or both of the other two species. Like them, it seems to occur as an epiphyll only in the wettest sites.

Schuster (1980) has provisionally placed *Cheilolejeunea principensis* into the synonymy of *C. rigidula* (Montagne) R. M. Schuster. If his treatment is confirmed by further investigation the epithet *rigidula* will have priority over *serpentina*.

6. **Cheilolejeunea surrepens** (Mitten) E. Jones in *J. Bryol.* **9**: 49 (1976).

Cheilolejeunea africana (Stephani) E. Jones in *Trans. Br. bryol. Soc.* **2**: 388 (1954).
Cheilolejeunea silvestris (Gottsche) E. Jones in *J. Bryol.* **7**: 548 (1973).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., epiphyllous, *Jones* s.n.; Toke, epiphyllous, *Jones* s.n. (these two specimens are sterile and named with slight doubt, though they are both the same species). Giema, forest near road, epiphyllous, *Harrington* 552b p.p., 552c p.p., 552d p.p.

GHANA. Pampramasi, on bole of small tree in forest, *Jones* 1408b. Aiyinasi A.R.S., on *Citrus, Jones* 1383 p.p.; on small tree by the Rest House, *Jones* 1363d. Pra-Suhien F.R., bough of small tree by the Rest House, *Jones* 1347b. Bunso, on cocoa, *Jones* 1317a p.p. Aiyaola F.R. near Kade, branches in crown of large *Piptadeniastrum, Jones* 1236 p.p.; branchlets in crown of *Khaya, Jones* 1237a; on bole of middle-storey tree, *Jones* 1239b. Kpedze, on cocoa, *Jones* s.n.

Cheilolejeunea surrepens is a variable species which is widely distributed in both West and East Africa, but usually forms very small colonies. It is often mixed with *C. intertexta* or *C. serpentina,* and slender branches may be difficult to distinguish from *C. intertexta,* though on strong shoots the much longer lobules are distinctive. It appears to be one of those species which are characteristically inhabitants of the smaller branches and twigs in the forest canopy, but which can also occur near the ground on the twigs of bushes and small trees in open places. Thus it tends to be collected around forest rest houses and in plantations. The paucity of records from Sierra Leone may be due to the lack of collections from suitable sites. It is very rarely epiphyllous, so that it is all the more remarkable that it has been recorded from Sierra Leone only as an epiphyll.

7. **Cheilolejeunea trifaria** (Reinw., Blume & Nees) Mizutani in *J. Hattori bot. Lab.* **27**: 132 (1964); Grolle in *Wiss. Z. Friedrich-Schiller-Univ. Jena* **27**: 9 (1978).

Euosmolejeunea brachytoma (Gottsche) Stephani, *Sp. hepat.* **5**: 577 (1914).

SIERRA LEONE. Freetown Peninsula: Leicester Peak, *Brenan* (*Jones* 476 p.p.); Sugar Loaf, 460 m (1500 ft), *T. S. Jones* 245 p.p. Lake Sonfon, on trunk of *Erythrophleum* at edge of forest, *Harrington* 53 p.p. Loma Mountains, Seradu, tree boles in valley forest by the village, *Jones* 1515b, 1516b. Kambui Hills, Bambawo, shaded earth bank, *Harrington* 508 p.p., *Jones* 1529 p.p.; tree bole by road, *Harrington* 570 p.p., *Jones* 1550 p.p.

GHANA. Ankasa River F.R., on bole of *Pentadesma, Richards* (GC 36674 p.p.). Aiyinasi A.R.S., on *Citrus* boles, *Jones* 1383d, e p.p. Ochi Headwaters F.R., *West-Skinn* 155, 183. Atewa Hills F.R., boughs in crown of *Lophira, Jones* 1319b. Aburi Botanical Gardens, on buttress of tree, *Jones* s.n. Between Vane and Amedzofe, rocks in steep roadside bank, *Jones* 1266a.

Cheilolejeunea trifaria has a wide but disjunct distribution in tropical Africa, which is difficult to understand. Where it is present it is often abundant. It tends to be montane – thus the records from the Freetown Peninsula are from the higher ground – but its occurrence nearly at sea-level in western Ghana suggests that this tendency may be determined by some factor such as the frequency of mists.

XVI. CHILOSCYPHUS Corda

1. **Chiloscyphus dubius** Gottsche in *Abh. naturw. Ver. Bremen* **7**: 346 (1882); E. Jones in *Trans. Br. bryol. Soc.* **2**: 200 (1953).

SIERRA LEONE. Freetown Peninsula, York Pass, on boulder on small island in stream, *Harrington* s.n. Gola North F.R., on rotten log by stream in forest, *Jones* 1566d (FBC).

GHANA. Ankasa River F.R., *Jones* s.n. (GC). Tarkwa, *Saxby*. Subri F.R., *Jones* ! Ochi Headwaters F.R., *West-Skinn* 184. Pra-Suhien F.R., on exposed tree root, *Jones* 1343 p.p. Esukawkaw F.R., *Jeník* (Herb. Jones). Begoro, below the waterfall, *Jones* ! Southern Scarp F.R., near Begoro, *Jones* ! Atewa Hills F.R., *Jones* 1331 p.p. (GC). Kade A.R.S., on stump in forest, *Hossain* (GC 36681). Amedzofe, *Irvine* 411, *Jones* s.n. (GC).

Chiloscyphus dubius is widely distributed and usually abundant in the lowland rain forests of West Africa, often associated with *Lophocolea martiana* subsp. *newtonii.* It also extends through East Africa to Natal, Madagascar, and the Mascarenes, but in these areas it is much more local, doubtless because of the very restricted occurrence of lowland forest with a sufficiently high rainfall. It usually grows on rotting wood in deep shade, but frequently also near the bases of trees and exposed tree roots. It is evidently frequent throughout the forests of southern Ghana. The paucity of records from Sierra Leone is remarkable; it may be explained at least in part by the fact that *C. dubius* is a lowland species (though in Ghana it is frequent up to 700 m) and is strictly confined to forest habitats. Little lowland forest survives in Sierra Leone, and we have few collections of hepatics from that which is left. In the Freetown Peninsula the rarity of *C. dubius* may be due to the long dry season, though the lowland forest here is mostly farm bush, which does not provide the decaying logs and the sheltered conditions that the species seems to need.

XVII. **COLOLEJEUNEA** (Spruce) Schiffner

1. **Cololejeunea africana** (Stephani) R. M. Schuster in *Beih. nov. Hedwigia* **9**: 173 (1963).

Leptocolea africana (Stephani) E. Jones in *Trans. Br. bryol. Soc.* **2**: 148 (1953).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., *Morton* s.n. (Herb. Jones); Toke, *Jones* s.n. Gola Hills, near Lalehun, on low vegetation, *Marshall* s.n.

Apparently a rare epiphyllous species, previously known only from a few gatherings in Cameroon and São Tomé, and from the mountains of south-eastern Kenya and eastern Tanzania (Bizot & Pócs, 1974, 1979). It is present in only very small amounts in the Sierra Leone collections.

2. **Cololejeunea androphylla** E. Jones in *Trans. Br. bryol. Soc.* **2**: 432 (1954).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., on rough bole of a large tree 12 cm from ground, *Jones* 1424. Kambui Hills, Bambawo, in forest on plateau, 370 m (1200 ft), on charred stump, *Jones* 1546, and on rotten log, *Jones* 1548. Gola Hills: Lalehun, log in forest, *Jones* s.n.; Gola North F.R., rotting log by stream in forest, *Jones* 1566c.

GHANA. Kade A.R.S., large rotten log in forest, *Jones* 1215a. Aiyaola F.R. near Kade, on rotten log, *Jones* 1230a.

Previously known from Nigeria and Cameroon (Jones, *op. cit.*), the Congo Republic (Pócs, 1980) and the Seychelles (Grolle, 1978).

3. **Cololejeunea appressa** (A. W. Evans) Benedix in *Beih. Repert. nov. Spec. Regni veg.* **134**: 31 (1953); E. Jones in *Trans. Br. bryol. Soc.* **5**: 571 (1968).

SIERRA LEONE. Giema, forest near road, epiphyllous, *Harrington* 552a p.p.

In continental Africa, hitherto known only from Uganda, Kenya (Bizot & Pócs, 1974), and Tanzania (Bizot & Pócs, 1979).

4. **Cololejeunea bolombensis** (Stephani) Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **42**: 475 (1972).

Leptocolea bolombensis (Stephani) E. Jones in *Trans. Br. bryol. Soc.* **2**: 155 (1953).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., on leaves of *Carapa procera*, *Harrington* s.n.; York Pass, low vegetation in forest, *Harrington* 633 p.p.; Picket Hill, in forest near summit, *c.* 850 m (2800 ft), *Gledhill* s.n. About five km south of Kabala, in secondary forest by road, *Harrington* 127 p.p. Lake Sonfon, in forest surrounding the 'lake', *Harrington* 33 p.p., 34, 35 p.p., 70e. Loma Mountains: forest above Sokurela, 1040 m (3400 ft), *Jones* 1514b; valley forest at Seradu, 610 m (2000 ft), *Jones* 1518. Kambui Hills, Bambawo, *Harrington* 467 p.p., 468 p.p., 483 p.p., *Jones* 1526, 1543a. Giema, in secondary forest, *Harrington* 548 p.p., 549a p.p. Gola Hills, near Lalehun, low vegetation in primary (?) forest, *Marshall* s.n.

In all the Sierra Leone collections *Cololejeunea bolombensis* was epiphyllous, on low vegetation in forest. The species is widely distributed, though perhaps local, in Africa from Guinea eastwards to Kenya, and southwards through the Congo Basin to the Uluguru Mountains in Tanzania, and, according to Pócs (Bizot & Pócs, 1979), the Umtali district of Rhodesia (= Zimbabwe). The absence of records from Ghana is, therefore, remarkable. In West Africa and the Congo Basin *C. bolombensis* is a lowland species, but the East African records come from altitudes of 900–2000 m, and thus indicate a montane taxon. Moreover, the closely allied *Cololejeunea adhaesiva* (Mitten) R. M. Schuster grows in the East African mountains.

Cololejeunea bolombensis is very variable, and it is likely that *Cololejeunea auriculata* (E. Jones) R. M. Schuster will prove to be an extreme form, with narrow lobules and faintly punctate cuticle. In many examples of *C. bolombensis*, including the type, the punctate cuticle is conspicuous but, as in many Lejeuneaceae with this form of cuticle (e.g. *Lejeunea flava* (Sw.) Nees), it varies greatly in distinctness, and the 'points' are sometimes so faint that careful observation with critical illumination is required to see them. The type of *C. auriculata* (*Jones* 73A) from Benin has a faintly punctate cuticle. The other differences from *C. bolombensis* are the width of the lobule, the insertion of the lobule, the extent of the hyaline border, and the general shape of the leaf (oval in *C. auriculata*, obovate in *C. bolombensis*).

5. Cololejeunea calcarata E. Jones, **sp. nov.** Figs 1 & 2.

Tenella; surculi cum foliis 0·6–1·0 mm lati, repentes. Folia 0·35–0·6 × 0·3–0·4 mm, contigua, antice secunda, semicirculares basi cuneata, margine postico stricto, margine antico arcuato, grosse 6–7 dentato dentibus triangulariis; dens distalis semper conspicuus, calcariforme retrocurvatus. Cellulae lobi laeves, medianae 15–20 × 20–30 μm, trigonis mediocris.

Lobulus quam lobo 1/2 brevior, oblongo-ovatus, proximale leviter inflatus, distale planus, carina stricta vel leviter arcuata, dens apicalis ex angulo lobuli oriens, vulgo bicellularis, (nonnunquam unicellularis), cellulo apicale sphaerico incurvo; papilla hyalina sphaerica 10–12 μm diametro in facie interno celluli basalis inserta, dens alter in margine libera subnullus.

Monoica. Bracteae masculae 3–4 jugae, laxe imbricatae, monandriae. Bracteae femineae lobis falcatis, apice acutis, interdum obscure dentatis; lobuli longitudine 2/3–3/4 loborum aequantes, anguste oblongi, apice acuti aut obtusi, carina substricta. Perianthium late pyriforme, 0·42 × 0·50 mm, dorso planum, ventre leviter inflatum, laterale obtuse carinatum, rostro brevissimo aut nullo.

Typus: Ghana, *Jones* 1355b, in Herb. Mus. Brit. conservatus.

Small and delicate, much branched, creeping on fronds of *Raphia* palm. Shoots 0·6–1·0 mm broad. Leaves approximate, arching upwards and forwards, 0·35–0·6 × 0·3–0·4 mm, nearly semicircular with cuneate base, broadly arched apex and antical margin, and straight or slightly concave postical margin. Apex and antical margin dentate with 4–7 distant large triangular teeth, very variable in size, but with the distal tooth at the junction of apex and postical margin always large and directed backwards, at right angles to the postical margin. Cells smooth, trigones medium, straight-sided or convex, intermediate thickenings occasional on some of the longer walls, chiefly in the mid and proximal part of the leaf; median cells 15–20 × 20–30 μm, cells of third and fourth rows from antical margin 14–15 × 15–22 μm.

Lobule large, with the slightly arched keel extending half the distance from insertion to apex of lobe, *c.* 250–300 × 125–150 μm, oblong-oval, moderately inflated proximally, plane distally, the free margin mostly visible in situ for about half its length, the apex usually truncate with a tooth at the angle, but very variable, and the angle sometimes extended to form a triangular lobe. The apical tooth mostly of two cells, the apical cell spherical and strongly incurved when mature, the hyaline papilla spherical, 10–12 μm diam., on the proximal half of the inner face of the basal cell of the tooth. An obscure blunt tooth sometimes present on the free margin, separated from the apical tooth by 3–4 cells. Stylus not found.

Stem 45–50 μm diam., the cortical cells 20 × 40–50 μm; in transverse section five cortical cells and one medullary cell, all uniformly rather thick walled.

Monoecious. Male bracts in 3–4 pairs, making a slender lax spike, the bracts monandrous; antheridia 50–55 μm diam. Female bracts resembling the leaves but narrower (*c.* 450 × 200 μm), and with longer lobules, falcate, irregularly and variably dentate, often entire except for the acute outwardly directed apex; lobule *c.* 2/3–3/4 the length of the lobe, the keel 1/2–2/3 its length, nearly straight, the ligulate apex truncate, rounded or acute. Perianth broadly pyriform, 0·5 × 0·4 mm, subcompressed, plane dorsally, ventrally inflated, ecarinate or the margin bluntly keeled around the apex and distally.

GHANA. Subri F.R., in swamp forest, on dead fronds of *Raphia,* with *Caudalejeunea africana, Colura digitalis, Cololejeunea crenatiflora, C. nigerica, Diplasiolejeunea cornuta, Cheilolejeunea surrepens,* etc., *Jones & Hall* (*Jones* 1355b; BM, holotype).

Cololejeunea calcarata is very distinct from *C. dentata,* the only other *Cololejeunea* with coarsely dentate leaves known from West tropical Africa; the two plants were indeed growing together.

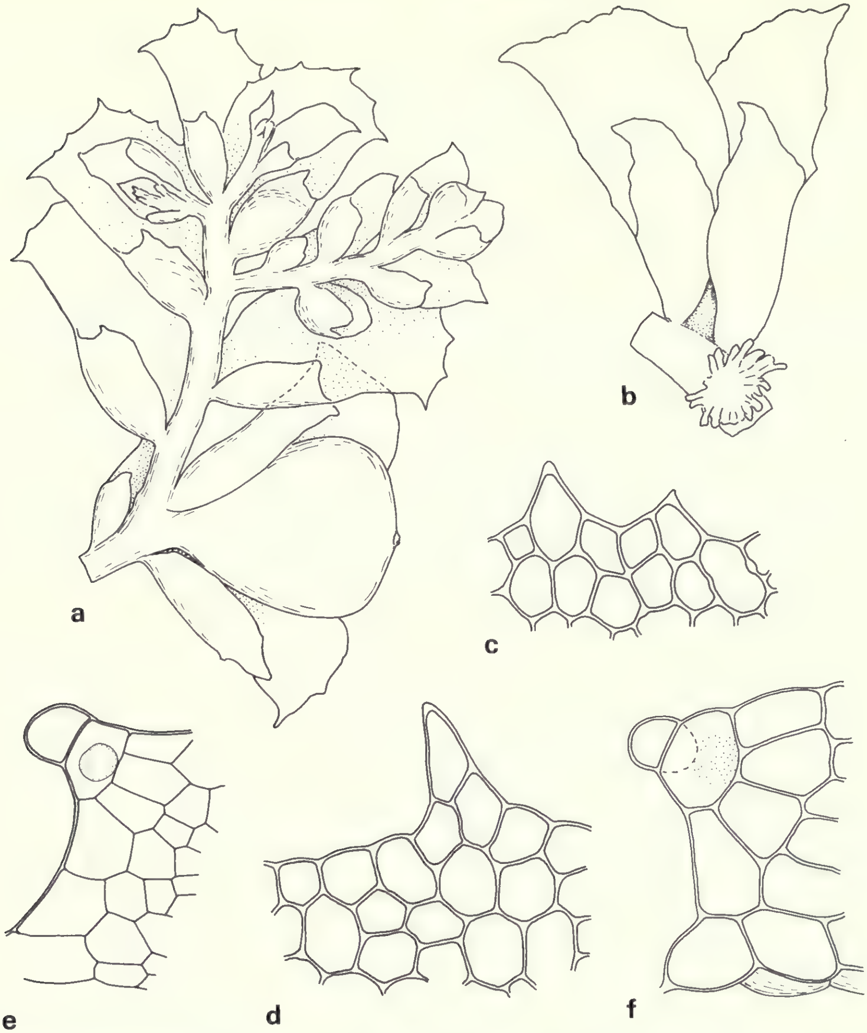

Fig. 1 *Cololejeunea calcarata* E. Jones. (a) shoot with perianth, ×60; (b) female bracts, ×100; (c) tooth 'w' and (d) tooth 'x' from leaf (a) in Fig. 2, ×500; (e) apical tooth of young lobule; (f) apical tooth of mature lobule, both ×500. Drawn from *Jones* 1355b (holotype).

Though they resemble each other in the general shape of the leaf, they differ in the pattern of dentition and in the tendency shown by *C. dentata* (in common with the allied *C. malanjae* Stephani from East Africa, *C. cuneifolia,* and others) to produce cells in the leaves, and even more in the perianths, which are conically protuberant and capped by lenticular thickenings of the wall. Thus in *C. dentata* the leaf margin between the major teeth is irregularly (though only slightly) crenulate or serrulate with protuberant cells, and slight lenticular thickenings of the wall can often be detected above the lumina of some of the other cells of the lobe. *C. calcarata* shows no trace of this tendency on either leaves or perianth. The postical margin of the leaf of *C. calcarata* is straight or slightly concave, and completely without teeth except for the large backwardly directed spur at its apex, whereas the postical margin in *C. dentata* tends to be convex with some minor denticulation. *C. malanjae* differs from *C. calcarata* even more in the shape of the leaf.

Judging from descriptions and drawings *Cololejeunea calcarata* resembles *C. plagiochiliana* P. Tixier from Madagascar in the shape of leaf, but has a very different perianth.

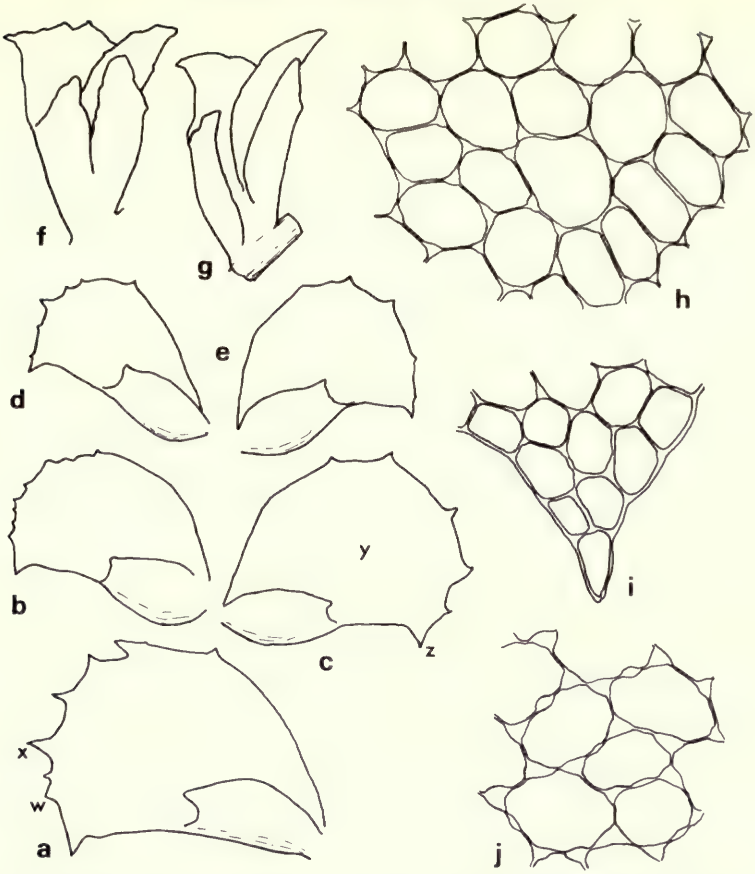

Fig. 2 *Cololejeunea calcarata* E. Jones. (a)–(e) leaves, ×60 – 'w' and 'x', teeth illustrated in Fig. 1 (c) and (d); (f), (g) female bracts, ×60; (h) cells from 'y' and (i) the tooth 'z' on leaf (c), ×500; (j) median cells from another leaf, ×500. Drawn from *Jones* 1355b (holotype).

6. Cololejeunea cardiocarpa (Montagne) R. M. Schuster in *Bryologist* **62**: 54 (1959); Vanden Berghen in *Revue bryol. lichén.* **44**: 448 (1978).

Leptocolea cardiocarpa (Montagne) A. W. Evans in *Bull. Torrey bot. Club* **38**: 268 (1911); E. Jones in *Trans. Br. bryol. Soc.* **3**: 200 (1957).

SIERRA LEONE. Freetown Peninsula, on branch of small bush by Mountain Torrent, *Jones* s.n.

A pantropical species, usually epiphyllous, which has not hitherto been recorded from West Africa, though it is widely distributed but apparently local from Cameroon (Tixier, 1975) and Zaire eastwards to Kenya and Tanzania, and south to Zimbabwe. As Vanden Berghen (*op. cit.*) notes, it tolerates considerable desiccation, and sometimes grows where no other epiphyllous species is present. Like many other epiphyllous species, it tends to be corticolous where dry conditions prevent the growth of epiphyllous communities. Its occurrence in the Freetown Peninsula is doubtless related to the severe dry season that the Peninsula experiences.

7. Cololejeunea cornuta E. Jones in *Trans. Br. bryol. Soc.* **2**: 436 (1954).

SIERRA LEONE. Gola North F.R., epiphyllous on low vegetation, *Jones* 1567 p.p., 1568 p.p.
GHANA. Ankasa River F.R., on low shrubs near the river, *Jones* 1375 p.p.

Previously known only from the Kwa Falls, Calabar, Nigeria.

8. Cololejeunea crenatiflora (Stephani) Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **42**: 487 (1972).

Leptocolea crenatiflora Stephani, *Sp. hepat.* **5**: 842 (1916); E. Jones in *Trans. Br. bryol. Soc.* **2**: 411 (1954).

SIERRA LEONE. Freetown Peninsula, Leicester Peak, in forest *c.* 60 m below the summit, *Jones* 1428 p.p. Kambui Hills, Bambawo, low vegetation by pool in forest, *Harrington* 468 p.p., 469 p.p., 474 p.p., 483 p.p., 484 p.p.

GHANA. Krokosua Hills F.R., leaves of low shrubs in forest, 490–550 m (1600–1800 ft), *Jones* 1396 p.p. Ankasa River F.R., low shrubs near the river, *Jones* 1375 p.p.; on palm leaves in swamp forest one mile south of the Ankasa bridge, *Jones* 1382. Subri F.R., on *Raphia* fronds in swamp forest, *Jones* 1355 p.p. Pra-Suhien F.R., *Jones* 1345b. Kade A.R.S., the dominant epiphyllous hepatic on herbs in wet places in forest, *Jones* 1221. Atewa Hills F.R., abundant in swamp forest, *Jones* 1294. Amedzofe, abundant on aroids beneath dripping rocks, *Jones* s.n.

Cololejeunea crenatiflora is a widely distributed epiphyllous species in tropical Africa, from Sierra Leone eastwards to Tanzania and southwards to north-western Zambia (Pócs, 1975) and the Uluguru Mountains in Tanzania. In West Africa it is predominantly a lowland species, though it has been recorded as high as 1430 m on Mont Cameroun (Cameroon Mountain). It is especially abundant in wet places in forest, where it is sometimes one of the dominant epiphyllous species. The paucity of records from Sierra Leone is probably attributable to the lack of collections from suitable sites.

9. Cololejeunea cuneifolia Stephani ex A. W. Evans in *Bull. Torrey bot. Club* **38**: 253 (1911).

Leptocolea cuneifolia (Stephani ex A. W. Evans) A. W. Evans in *Bull. Torrey bot. Club* **38**: 280 (1911); Stephani, *Sp. hepat.* **5**: 843 (1916); E. Jones in *Trans. Br. bryol. Soc.* **2**: 414 (1954).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., *Harrington* 86 p.p., 91 p.p., 103 p.p., *Jones* 1423; Leicester Peak, *Jones* 1428 p.p.; Bathurst, Kongo Dam, *Jones* s.n.; Guma Valley, mature forest, *Harrington* 101 p.p., 112 p.p.; Toke, *Jones* s.n.; Black Johnson Beach near York, thicket behind the beach, *Harrington* 15; York Pass, forest understorey, *Harrington* 625 p.p., 630 p.p.; Picket Hill, forest near summit, *c.* 850 m (2800 ft), *Gledhill* s.n. Lake Sonfon, on herbs in forest surrounding the 'lake', *Harrington* 70 p.p. Masimo, *Marmo* 160 p.p., 161 p.p. Kambui Hills, Bambawo, *Harrington* 411, 484 p.p., *Jones* 1526 p.p., 1543 p.p. Giema, secondary forest, *Harrington* 528 p.p., 549a p.p. Gola Hills, near Lalehun, *Marshall* s.n., by stream in forest, *Jones* 1567.

GHANA. Krokosua Hills F.R., frequent on low shrubs in small gaps in forest, 490–550 m (1600–1800 ft), *Jones* 1396. Ankasa River F.R., low herbs and small shrubs near the river, *Jones* 1374b, 1375 p.p. Pra-Suhien F.R., frequent on herbs, *Jones* 1345c p.p.

Cololejeunea cuneifolia often accompanies *C. crenatiflora* and is likewise often one of the most abundant epiphyllous hepatics in moist, sheltered places on herbs and low shrubs in the forest. The relative abundance of *C. cuneifolia* in Sierra Leone and its scarcity in Ghana is remarkable, and may perhaps indicate a preference for a somewhat different rainfall regime from that which favours *C. crenatiflora.*

Cololejeunea cuneifolia is very close to *C. duvignaudii* E. Jones and also to *C. zenkeri* (Stephani) E. Jones. Jones (*op. cit.*) followed Evans (*op. cit.*) and Stephani (*op. cit.*) in placing *C. cuneifolia* in *Leptocolea* – i.e. as having a compressed perianth – whereas he placed the other two species in *Cololejeunea,* though their perianths are plane dorsally and therefore subcompressed, and thus intermediate between the compressed perianths of *Leptocolea* and the fully terete perianths of *Cololejeunea sensu stricto. C. zenkeri* is sufficiently distinct from the other two in its small, spherical hyaline papilla situated at the base of the apical tooth; moreover it is a montane species. Vegetatively *C. cuneifolia* and *C. duvignaudii* resemble each other in having a pyriform hyaline papilla on the side, or near the apex, of the apical tooth. Jones described *C. cuneifolia* as having a lobule often greatly reduced, but always less than 1/3 the length of the lobe, measured from insertion to apex, whereas *C. duvignaudii* had lobules 1/4–2/5 the length of the lobe. The greater range of material now available shows that *C. cuneifolia* is considerably more variable than was implied in 1954. The length of the lobule ranges from 1/9 to 1/3·5 the length of the lobe, though in 80 per cent of the West African specimens it is 1/4 or less. The minority with lobules 1/3·5 the length of the lobe come from open sites on the Freetown Peninsula (*Harrington* 630 p.p., *Jones* 1428 p.p., Toke, *Jones* s.n.) and might be considered to be small-lobuled forms of *C. duvignaudii*, though they are clearly the same species as plants with smaller lobules from more sheltered sites on the Peninsula. The perianths of these large-lobuled Sierra Leone plants agree with *C. cuneifolia*. The lobules of the type collection of *C. duvignaudii* (*Duvignaud* 998c) vary from 1/3·7–1/2·4 of the length of the lobe. A review of all the available material suggests that *C. cuneifolia* is chiefly West African and north of the equator, while *C. duvignaudii* is exclusively south of the equator; the few records of *C. cuneifolia* from south of the equator may well be *C. duvignaudii* with reduced lobules. The leaves of *C. cuneifolia* frequently have papillae over one or more marginal rows of cells – a single papilla over the lumen of each cell. These papillae vary greatly in development; they may be detectable over the whole distal half of the leaf.

10. Cololejeunea dentata (E. Jones) R. M. Schuster in *Beih. nov. Hedwigia* **9**: 175 (1963).

Leptocolea dentata E. Jones in *Trans. Br. bryol. Soc.* **2**: 161 (1953).

SIERRA LEONE. Kambui Hills, Bambawo, low vegetation by pool in forest, *Harrington* 471 p.p.
GHANA. Subri F.R., epiphyll in *Raphia* swamp, *Jones* 1355a.

Apparently a rare species, known also from Mont Cameroun (Cameroon Mountain) and from Zaire (Kindu, *Jones* 798).

11. Cololejeunea elegans (Stephani) E. Jones in *Trans. Br. bryol. Soc.* **2**: 424 (1954).

Physocolea elegans Stephani, *Sp. hepat.* **5**: 870 (1916).

GHANA. Atewa Hills F.R., on tree boles in swamp forest (the 'Kaolin Swamp'), scattered in small amounts through mats of other bryophytes, *Jones* 1328 p.p., 1331 p.p.

A rare species, known otherwise only from the type collection in Cameroon (Bomana, *Dusen* 133) and from a recent collection on Kasigau Mtn, S.E. Kenya, by Faden (det. Pócs, Bizot & Pócs, 1974).

12. Cololejeunea floccosa (Lehm. & Lindenb.) Schiffner, *Consp. hepat. archip. ind.*: 243 (1898); E. Jones in *Trans. Br. bryol. Soc.* **5**: 571 (1968).

SIERRA LEONE. Gola Hills, near Lalehun, epiphyllous on low vegetation in primary (?) forest, *Marshall* s.n.

Probably the only record of this species from Africa.

13. Cololejeunea hyalino-marginata (Nees ex Montagne) Grolle in *J. Hattori bot. Lab.* **49**: 85 (1981).

Leptocolea leloutrei E. Jones in *Trans. Br. bryol. Soc.* **2**: 146 (1953).
Cololejeunea leloutrei (E. Jones) R. M. Schuster in *Beih. nov. Hedwigia* **9**: 173 (1963).

SIERRA LEONE. Gola North F.R., epiphyllous on herbs in unexploited primary forest, *Jones* 1568 p.p.
GHANA. Krokosua Hills F.R., 490–550 m (1600–1800 ft), epiphyllous on low shrubs in small gaps in forest, *Jones* 1396 p.p.

A variable epiphyllous species, hitherto known from Cameroon (Tixier, 1975), São Tomé, Kenya, and Tanzania where it is frequent on some of the mountains. It is also frequent in the Seychelles, the Comoro Islands, Madagascar, Réunion, and Mauritius (Grolle, *op. cit.*).

14. Cololejeunea lanceolata E. Jones in *Trans. Br. bryol. Soc.* **2**: 428 (1954).

SIERRA LEONE. Kambui Hills, Bambawo, *Marshall* (*Harrington* 475 p.p.); on very low vegetation in forest near pool, *Harrington* 558a.

GHANA. Ankasa River F.R., on low herbs in moist place in deep shade, *Jones* 1374a. Pra-Suhien F.R., local, *Jones* 1345a. Atewa Hills F.R., epiphyllous in swamp forest (the 'Kaolin Swamp'), *Jones* 1331b p.p.

Previously known only from Nigeria and Cameroon.

15. **Cololejeunea myriocarpa** (Nees & Montagne) A. W. Evans in *Bull. Torrey bot. Club* **38**: 256 (1911).

Cololejeunea minutissima subsp. *myriocarpa* (Nees & Montagne) R. M. Schuster in *J. Elisha Mitchell scient. Soc.* **71**: 232 (1955).

GHANA. Kade A.R.S., on branches of *Bauhinia* by the Rest House, *Jones* 1243a.

Only a single colony of this plant was seen; it seems to be without gemmae, but in other respects it closely matches *Cololejeunea myriocarpa,* a species known from the West Indies, Mexico and southern Florida. Plants which are closely allied, if not identical, are widely distributed, but apparently rare, in tropical and South Africa, and have given rise to considerable differences of opinion as to their taxonomic status. Amongst these is *C. myriantha* (Herzog) S. Arnell from South Africa. Arnell (1963) records it from many localities. The most important difference from *C. myriocarpa* noted by Herzog (1952) is its larger cells. *C. dissita* E. Jones (Jones 1954*b*) from Benin is a form which is, exceptionally, epiphyllous, and in which all the leaves have fully developed saccate lobules. *C. minutissima* subsp. *utriculifera* Vanden Berghen (Vanden Berghen, 1961) is distinguished chiefly by the presence of some leaves which take the form of 'utricles', the lobules being as large as, or larger than, the lobes; it has been recorded only from Rwanda at 2000–2400 m, and may perhaps be a montane form.

Schuster (*op. cit.*) considered *Cololejeunea myriocarpa* to be a subspecies of *C. minutissima* (Smith) Schiffner, but Tixier (1979) made them fully synonymous. I cannot accept Tixier's opinion. *C. minutissima* was described from Britain, where it is not a variable species, and appears to differ consistently from *C. myriocarpa* and its allies from tropical Africa in its larger lobules, which are almost always saccate (only occasionally does the basal leaf of a branch or the pair of leaves immediately below a female inflorescence have explanate lobules), its larger gemmae, and female bracts with a distinct sinus between lobe and lobule, and with a blunt keel. Schuster noted these differences in American material of the two species, though he found some overlapping in the range of number of cells in the gemmae. [E.W.J.]

The Ghana plant (and others that I have seen from Nigeria) cannot be ascribed to either *Cololejeunea myriantha* or to *C. minutissima* subsp. *utriculifera*. It seems to me that *C. myriocarpa* and *C. minutissima* are sufficiently distinct to make it a matter of no great importance whether the one is regarded as a subspecies of the other or not, and to maintain *C. myriocarpa* as a species makes nomenclature less cumbersome. The whole complex clearly needs critical revision on a world scale. [E.W.J.]

16. **Cololejeunea nigerica** (E. Jones) R. M. Schuster in *Beih. nov. Hedwigia* **9**: 177 (1963).

Leptocolea nigerica E. Jones in *Trans. Br. bryol. Soc.* **2**: 150 (1953).

SIERRA LEONE. Freetown Peninsula, York Pass, epiphyllous on low vegetation, *Harrington* 636 p.p. Three km south of Kabala, by the road to Makeni, in secondary forest, *Harrington* 126 p.p., 127 p.p. Bo, near the school, *Revell* (Herb. Jones). Kambui Hills, Bambawo, on leaves of mango, *Jones* 1541 p.p. (lobules atypical).

GHANA. Asenanyo F.R., on branches in crown of *Triplochiton, Jones* 1412 p.p., and in crown of *Terminalia superba, Jones* 1413a p.p. (form in which some leaves lack hyaline cells). Pra-Suhien F.R., on bough of tree by the Rest House, *Jones* 1347a p.p. Kade A.R.S., on twigs of *Citrus, Jones* 1226. Aburi Botanical Gardens, on stone, *Jones* s.n. (GC) and on *Bougainvillea* twigs, *Jones* s.n. Amedzofe, epiphyllous on herbs in cocoa farms above the waterfall, *Jones* 1273 p.p. Kpedze Rest House, on twigs of cocoa, *Jones* s.n.

Cololejeunea nigerica appears to be a West African lowland species. As the above records show it is frequent on the bark of twigs and small trees in open places, where it is probably often overlooked. Although it was first described as an epiphyllous species, it seems to be less frequent in this habitat.

17. Cololejeunea peraffinis (Schiffner) Schiffner, *Consp. hepat. archip. ind.*: 245 (1898), var. **elegans** Benedix in *Beih. Repert. nov. Spec. Regni veg.* **134**: 35 (1953); E. Jones in *Trans. Br. bryol. Soc.* **5**: 571 (1968).

SIERRA LEONE. Lake Sonfon, by seasonal stream in forest surrounding the 'lake', epiphyllous, *Harrington* 70b p.p.

18. Cololejeunea pusilla Stephani in *Hedwigia* **34**: 251 (1895); E. Jones in *Trans. Br. bryol. Soc.* **2**: 426 (1954), var. **pusilla**

GHANA. Southern Scarp F.R., near Begoro, on small barkless smooth log in moderate shade, *Jones* 1305.

var. **obtusifolia** E. Jones in *Trans. Br. bryol. Soc.* **2**: 427 (1954).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., *Harrington* 103 p.p.; *Jones* 1423; Guma Valley. mature forest, *Harrington* 112 p.p.; Black Johnson Beach near York, in thicket behind the beach, *Harrington* s.n.; York Pass, on low vegetation, *Harrington* 636 p.p.; Picket Hill, in forest near summit, 850 m (2800 ft), *Gledhill* s.n. About five km south of Kabala, secondary forest, *Harrington* 126 p.p., 127 p.p. Lake Sonfon, on herbs and small shrubs in forest surrounding the 'lake', *Harrington* 35 p.p., 44, 45, 70 p.p., 70c, 70d, 70e. Loma Mountains: between Kurubonla and Seradu, in forest by stream, *Harrington* 141; Seradu, in forest in valley by the village, *c.* 610 m (2000 ft), *Jones* 1518 p.p.; forest above Sokurela, *Harrington* 385 p.p., and at 1040 m (3400 ft), *Jones* 1514b p.p.; near 'Camp 1', *c.* 1220 m (4000 ft), on *Marattia* by stream, *Harrington* 292d p.p. Kambui Hills, forest above Bambawo, *Harrington* 421 p.p., 485 p.p., *Jones* 1526 p.p., 1543 p.p. Giema, secondary forest, on low vegetation, *Harrington* 528 p.p. Jawo, bank of the river Moa, on branches of tree at top of, or just above, the flood level, *Jones* 1536. Gola Hills: Lalehun, in forest by stream, *Jones* s.n.; near Lalehun, on low vegetation in primary (?) forest, *Marshall* s.n.

GHANA. Krokosua Hills F.R., 490–550 m (1600–1800 ft), abundant on leaves of low shrubs in small gaps in forest, *Jones* 1396 p.p. Ankasa River F.R., on low shrubs in small gap in forest, *Jones* 1375 p.p. Begoro, on rocks in dry stream bed below the waterfall, in light-canopied forest, *Jones* 1307c. Atewa Hills F.R., on low herbs, *Jones* 1294 p.p.

The relationship between *Cololejeunea pusilla* var. *pusilla* and var. *obtusifolia* requires further study; the two sometimes grow together, and intermediates sometimes occur, but var. *obtusifolia* is apparently always much the more abundant. Both are almost always epiphyllous, though occasionally occurring on other substrata. Var. *obtusifolia* is one of the most widely distributed epiphyllous hepatics in tropical Africa, often being the only epiphyllous species present in districts that are climatically marginal for their occurrence. It is, however, mainly a species of lowland forest; thus in the Loma Mountains it is frequent at 1000–1200 m, but has not been recorded from the higher forests of the plateau. Unlike some relatively drought-tolerant epiphyllous Lejeuneaceae which can grow in the crowns of forest trees, *C. pusilla* seems to be restricted to leaves of herbs and low shrubs. Like many other epiphyllous hepatics, it often grows near water. Perianths are relatively uncommon.

19. Cololejeunea zenkeri (Stephani) E. Jones in *Trans. Br. bryol. Soc.* **2**: 420 (1954).

SIERRA LEONE. Loma Mountains: forest near 'Camp 1', 1220 m (4000 ft), *Harrington* 289 p.p., and on *Marattia* by stream, *Harrington* 292d p.p.; valley forest near 'Camp 2', 1520–1680 m (5000–5500 ft), *Morton* (*Harrington* 364 p.p.), *Jones* 1483a p.p., *Jones* 1488.

Cololejeunea zenkeri is closely related to *C. cuneifolia*; both have leaves of the same general shape and with the same type of marginal dentition and areolation. *C. zenkeri* is, however, quite distinct in having a spherical (not pyriform) hyaline papilla on the inner face of the base of the apical tooth (not on the side of the tooth). It appears to be strictly a montane species, occurring at higher altitudes than *C. cuneifolia*, probably in all the main groups of tropical African mountains eastwards to Tanzania.

XVIII. **COLURA** (Dumort.) Dumort.

1. **Colura digitalis** (Mitten) Stephani, *Sp. hepat* **5**: 931 (1916); E. Jones in *J. Bryol.* **10**: 387 (1979).

SIERRA LEONE. Freetown Peninsula, three km north-east of Toke, epiphyllous, *Jones* s.n. Loma Mountains: gallery forest *c.* one km west of 'Camp 2', 1520 m (5000 ft), *Morton* (*Harrington* 347 p.p., 354); bushes by spring by 'Camp 2', 1680 m (5500 ft), *Jones* 1495a. Kambui Hills, Bambawo, low vegetation by pool in forest, *Harrington* 472 p.p.

GHANA. Ankasa River F.R., on twigs in crown of *Samanea* by the river, rare, *Jones* 1377b p.p. Subri F.R., on leaves of *Raphia* in swamp forest, *Jones* 1355 p.p. Atewa Hills F.R., epiphyllous in swamp forest (the 'Kaolin Swamp'), *Jones* 1331b p.p.

2. **Colura dusenii** (Stephani) Stephani, *Sp. hepat.* **5**: 931 (1916); E. Jones in *J. Bryol.* **10**: 387 (1979).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., on *Eugenia jambos, Harrington* 750 p.p., in forest in valley bottom, *Jones* s.n.; York Pass, in forest by stream, *Harrington* 612 p.p., 614 p.p.

GHANA. Ankasa River F.R., abundant on twigs in crown of *Samanea* by the river, *Jones* 1377 b p.p.; on leaves of undergrowth in moist gully, *Richards* R7054 p.p. (Herb. Jones). Subri F.R., on *Raphia* fronds in swamp forest, *Jones* 1355 p.p.

Colura digitalis and *C. dusenii* sometimes grow together, as in *Jones* 1355 and 1377, but whereas *C. digitalis* is generally distributed in suitable localities throughout tropical Africa, and extends to the Comoro Islands, *C. dusenii* is very much more local. Both species may be epiphyllous or grow on twigs and branchlets, and both occur through a wide altitudinal range.

3. **Colura tenuicornis** (A. W. Evans) Stephani, *Sp. hepat.* **5**: 942 (1916).

Colura calyptrifolia subsp. *tenuicornis* (A. W. Evans) Vanden Berghen in *Bull. Soc. r. Bot. Belg.* **42**: 463 (1972).

SIERRA LEONE. Kambui Hills, Bambawo, low vegetation by pool in forest, *Harrington* 472 p.p.; on mango leaves near the ground, *Jones* 1541 p.p.

XIX. **CONOSCYPHUS** Mitten

1. **Conoscyphus trapezioides** (Sande Lacoste) Schiffner in Engl. & Prantl, *Nat. Pflanzenfam.* **1** (3): 92 (1893).

Lophocolea devexa Mitten in *J. Proc. Linn. Soc.* **7**: 165 (1863 ['1864']).

SIERRA LEONE. Loma Mountains, on boles of large *Parinari excelsa* on the margin of the forest, 1520–1680 m (5000–5500 ft), locally common, but sometimes as extremely slender shoots creeping amongst other bryophytes, *Jones* 1477a, 1490.

Previously known in Africa only from Mont Cameroun (Cameroon Mountain), São Tomé, and more recently from the Uluguru Mountains in Tanzania (Bizot & Pócs, 1974), but with a disjunct distribution in the mountains of the Mascarenes, the Indo-Malayan region, and Samoa.

XX. **CYATHODIUM** Kunze

1. **Cyathodium africanum** Mitten in *J. Linn. Soc.* (Bot.) **22**: 327 (1886); E. Jones in *Trans. Br. bryol. Soc.* **2**: 58 (1952).

SIERRA LEONE. Freetown Peninsula: Mount Aureol, path below Kortright, in very sheltered rock crevice, *Harrington* 664; Leicester, vertical bank of ferruginous stone by road, 400 m (1300 ft), *Jones* 1450; Regent, beside stream, *Irvine* 222; by path from Regent to the Sugar Loaf, on brick supports of pipeline in forest, *Harrington* 645. Musaia Agricultural Station, on bare ground near the Rest House, *Haswell* B17 (sterile). Near road-bridge over tributary of the Rokel River, *c.* 32 km (20 miles) south-west of Kabala, on earth bank, *Harrington* 402 (sterile). Kambui Hills, Bambawo, on stonework below bridge, *Harrington* 562 (sterile). Sunkori, 19 km south of Kurubonla (9°02′N, 11°01′30″W), by stream, *W. N. Woodhead* (Herb. Richards).

GHANA. Mpraeso Scarp, *Hall* 2644. Amedzofe Mission House, *Irvine* 403.

Doubtless far more widely distributed, especially in Ghana, than the records indicate. It appears to need a seasonally wet and nutrient-rich substratum, and often grows in deep shade, when it is rendered conspicuous by the brilliant luminous emerald green of the young thalli. It dies in the dry season. It frequently grows in man-made habitats, e.g. drains in villages. It is probably conspecific with the South American *Cyathodium cavernarum* Kunze.

XXI. **CYLINDROCOLEA** R. M. Schuster

1. **Cylindrocolea atroviridis** (T. Sim) Váňa in *Lejeunia* II, **98**: 7 (1979).

Cephaloziella atroviridis (T. Sim) S. Arnell in *Bot. Notiser* **108**: 309 (1955); E. Jones in *Trans. Br. bryol. Soc.* **3**: 431 (1958).

SIERRA LEONE. About five km south of Kabala, in forest by the Makeni road, on fallen partly burned tree, *Harrington* 124.

GHANA. Afram Headwaters F.R., on rotting logs in plantation, *Jones* 1416.

Widely distributed in tropical Africa, but chiefly in climates with a strong dry season, and especially, as near Kabala, on wood that has been charred. Thus it is likely to be frequent in the drier parts of both Ghana and Sierra Leone where very few bryophytes have been collected.

2. **Cylindrocolea chevalieri** (Stephani) R. M. Schuster in *Bull. natn. Sci. Mus. Tokyo* **12**: 666 (1969); E. Jones in *J. Bryol.* **9**: 46 (1976).

Alobiella chevalieri Stephani, *Sp. hepat.* **3**: 351 (1908).
Cephaloziella retusa E. Jones in *Trans. Br. bryol. Soc.* **3**: 438 (1958).

GHANA. Begoro, on wet rocks and on rotting log at edge of stream close to water level just above the waterfall, *Jones* 1311a & b. Amedzofe, on wet rocks, sheltered but well lit, in stream just above the waterfall, *Jones* 1278e; also sterile, depauperate and scanty at the foot of cliff just below summit of the hill, *Jones* !

Previously known only from single records from Brazzaville on the Congo, the Falls of the Mougoungoulou in Gabon, and Idanre in western Nigeria. See Jones (*op. cit.*) for details.

3. **Cylindrocolea ?ugandica** (E. Jones) R. M. Schuster in *Nova Hedwigia* **22**: 171 (1972 ['1971']).

Cephaloziella ugandica E. Jones in *Trans. Br. bryol. Soc.* **3**: 433 (1958).

SIERRA LEONE. Loma Mountains, on bole of large tree on forest margin close to 'Camp 2', 1680 m (5500 ft), probably occasionally scorched, *Jones* 1476a p.p.

This plant resembles *Cylindrocolea ugandica* in perianth, but differs in having a more shallowly lobed leaf with a broader insertion. In this respect it resembles an un-named sterile plant from Uganda in Herb. Jones (Murchison Falls, *Gittins* 19). These two plants may represent an undescribed species. It is, however, clear that this complex, which includes also *C. gittinsii* (E. Jones) R. M. Schuster, *C. madagascariensis* (Stephani) R. M. Schuster, and *Cephaloziella abyssinica* Gola, requires critical revision with the aid of more copious collections than are at present available.

XXII. **DICRANOLEJEUNEA** (Spruce) Schiffner

1. **Dicranolejeunea madagascariensis** (Gottsche) Stephani, *Sp. hepat.* **5**: 158 (1912); E. Jones in *Trans. Br. bryol. Soc.* **6**: 73 (1970), var. **madagascariensis**

SIERRA LEONE. Loma Mountains: forest near 'Camp 1', *c.* 1220 m (4000 ft), on tree bole, *Harrington* 264 p.p.; valley north-west of Bintimani, on stem of liane in deep shade, *Jones* 1498c; west-facing cliffs of Bintimani, *c.* 1830 m (6000 ft), on rock face, *Harrington* 213.

Previously known from Cameroon, East Africa, and Madagascar.

XXIII. DIPLASIOLEJEUNEA (Spruce) Schiffner

1. **Diplasiolejeunea aulae** E. Jones in *J. Bryol.* 7: 552 (1973).

GHANA. Atewa Hills F.R., boughs in crown of *Lophira, Jones* 1319c (BM, type); upper part of bole of *Antiaris africana, Jones* 1320 p.p.

2. **Diplasiolejeunea cavifolia** Stephani in *Bot. Jb.* **20**: 318 (1895); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **47**: 220 (1977).

Diplasiolejeunea brachyclada A. W. Evans in *Bull. Torrey bot. Club* **39**: 216 (1912); Grolle in *Feddes Reprium* **73**: 86 (1966).

GHANA. Aiyaola F.R. near Kade, on branches and twigs in crown of *Piptadeniastrum, Jones* 1236 p.p., and on branches and twigs of *Khaya, Jones* 1237 p.p.

3. **Diplasiolejeunea cornuta** Stephani, *Sp. hepat.* **5**: 918 (1916); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **47**: 221 (1977). Fig. 3.

GHANA. Aiyinasi A.R.S., on *Citrus* leaves, *Jones* 1385a. Subri F.R., on *Raphia* leaves in swamp forest, *Jones* 1355 p.p.

Diplasiolejeunea cornuta is widely distributed but apparently local in tropical Africa. It is a variable plant; the type, illustrated by Vanden Berghen (1960*a*), has entire leaves with a rounded apex, ('marginibus repandis vel erosulis' according to Stephani (*op. cit.*)) but forms are frequent in which the leaves are more or less dentate, as illustrated by Jones (1973) and Vanden Berghen (1977). *Jones* 1385a differs in several respects from other dentate-leaved forms of the species that I have seen from Africa, and may prove to be a distinct species, although Grolle considers (*in litt.*) that it falls within the range of variation of *D. cornuta*. Usually in dentate forms of *D. cornuta* the postical margin of the lobe is arched and makes a well marked angle with the keel, and it bears one or two blunt teeth at its proximal base, quite close to the keel; the teeth on the antical margin are very irregular, and many are formed by strongly protuberant single cells. In *Jones* 1385a the postical margin is straight, almost in line with the keel, and entire except for a strong triangular spur-like backwardly directed tooth at its apex. The antical margin bears three or four similar evenly-spaced triangular teeth. The group of ocelli at the base of the leaf consists of up to ten cells (usually two to five in *D. cornuta*), and the ocelli are brown. [E.W.J.]

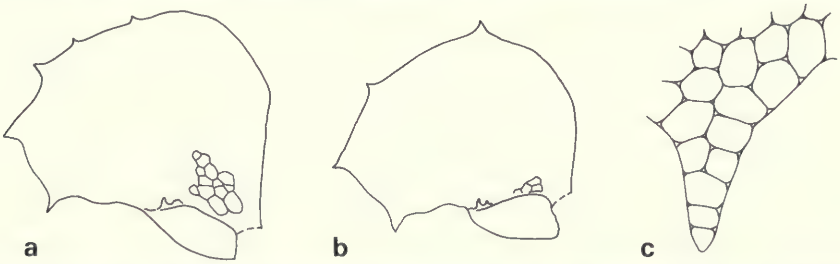

Fig. 3 *Diplasiolejeunea cornuta* Stephani forma. (a), (b) leaves, ×60; (c) tooth at distal end of postical margin of leaf, ×300. Drawn from *Jones* 1385a.

4. **Diplasiolejeunea harpaphylla** Stephani, *Sp. hepat.* **5**: 919 (1916).

Diplasiolejeunea incurvata Jovet-Ast & P. Tixier in *Revue bryol. lichén.* **31**: 29 (1962); fide Grolle *in litt.*

SIERRA LEONE. Kasewe F.R., on savanna tree amongst *Calymperes* sp., *Richards* s.n. (Herb. Jones).
GHANA. Ankasa River F.R., on twigs in crown of *Samanea* by the river, *Jones* 1377b. Aiyinasi A.R.S., on bough of small tree by the Rest House, *Jones* 1384b. Asenanyo F.R., twigs in crown of *Terminalia superba, Jones* 1413a p.p. Pra-Suhien F.R., on bough of *Acacia* by the Rest House, *Jones* 1347a. Aiyaola F.R. near Kade, twigs and branchlets in crown of *Piptadeniastrum, Jones* 1236 p.p., and in crown of *Cylicodiscus, Jones* 1240.

XXIV. **DREPANOLEJEUNEA** (Spruce) Schiffner

1. **Drepanolejeunea ankasica** E. Jones, **sp. nov.** Figs 4 & 5.

Monoica. Folia aliquantum falcata, apice late acuto, decurvo, margine subintegro aut irregulariter obtuseque dentata, basi antica proximale stricta, distale arcuata, caulem excedente. Cellulae medianae 24–36 × 15–18 μm, parietibus vix incrassatis; ocelli tres uniseriati adsunt, ocellis duobus basalibus contiguis, tertio superiore sejuncto. Lobulus fusiformis margine libero incurvo, ex quatuor cellulis constructo, dente apicali longe libero, curvato. Amphigastria obtrapeziformia, quam caule 2–2½-plo latiora lobis latis, acutis, patulis, sinu latissimo, basi cuneata.

Perianthium circa 0·5 × 0·35 mm, obconicum, quinquecarinatum, carinis altis, distale crenulatodentatis.

Typus: Ghana, Ankasa River Forest Reserve, *Jones* 1377 pro parte, in Herb. Mus. Brit. conservatus.

Green, creeping over twigs. Stem 45–60 μm diam. with cortical cells *c.* 18 × 35 μm. Leaves approximate to imbricate, 0·23–0·26 mm long × 0·2–0·3 mm wide, antically secund, more or less falcate with decurved acute but rather widely pointed apex; antical base proximally straight and parallel to the stem, then arching across the stem and passing into the arched antical margin, the postical margin concave, the apex ending in a single short cell, rather widely or even bluntly pointed; the margin nearly entire or the antical margin irregularly dentate with up to 6–8 low, obtuse, irregularly spaced teeth, each formed by a conically protuberant cell.

Lobule fusiform, about two fifths the length of the lobe, the free margin incurved, not visible *in situ*, of four cells; the apical tooth long (*c.* 30 × 8μm), curved, acute, free for most of its length with the large hyaline papilla near its base on the proximal side, lying against the margin of the lobule, the tip of the apical tooth engaging with protuberant cells on the inner face of the lobe.

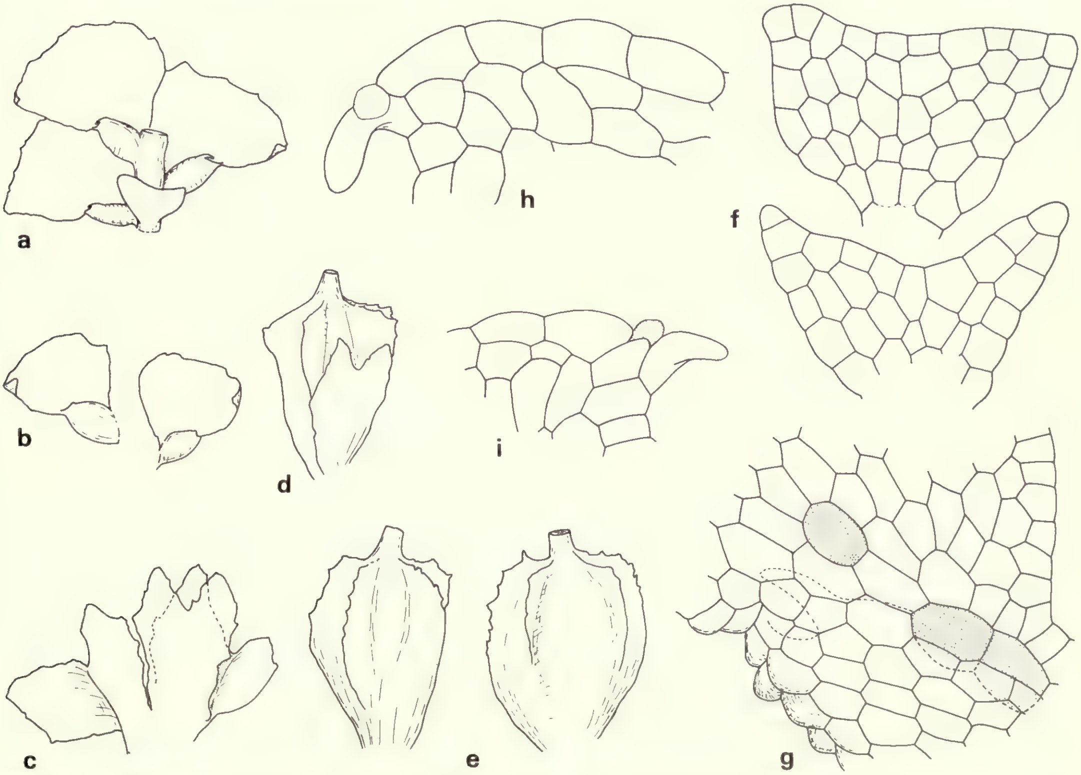

Fig. 4 *Drepanolejeunea ankasica* E. Jones. (a) part of shoot; (b) leaves; (c) female involucre; (d) perianth with bracteole; (e) perianths. All ×56. (f) underleaves, ×280; (g) base of leaf, antical view, ×280 – keel of lobule and its junction with the lobe to the left, the basal ocelli partly overlapped by adjacent cells; (h) apical tooth and free margin of lobule, ×470; (i) apical tooth of lobule, ×470. All drawn from *Jones* 1377 (holotype).

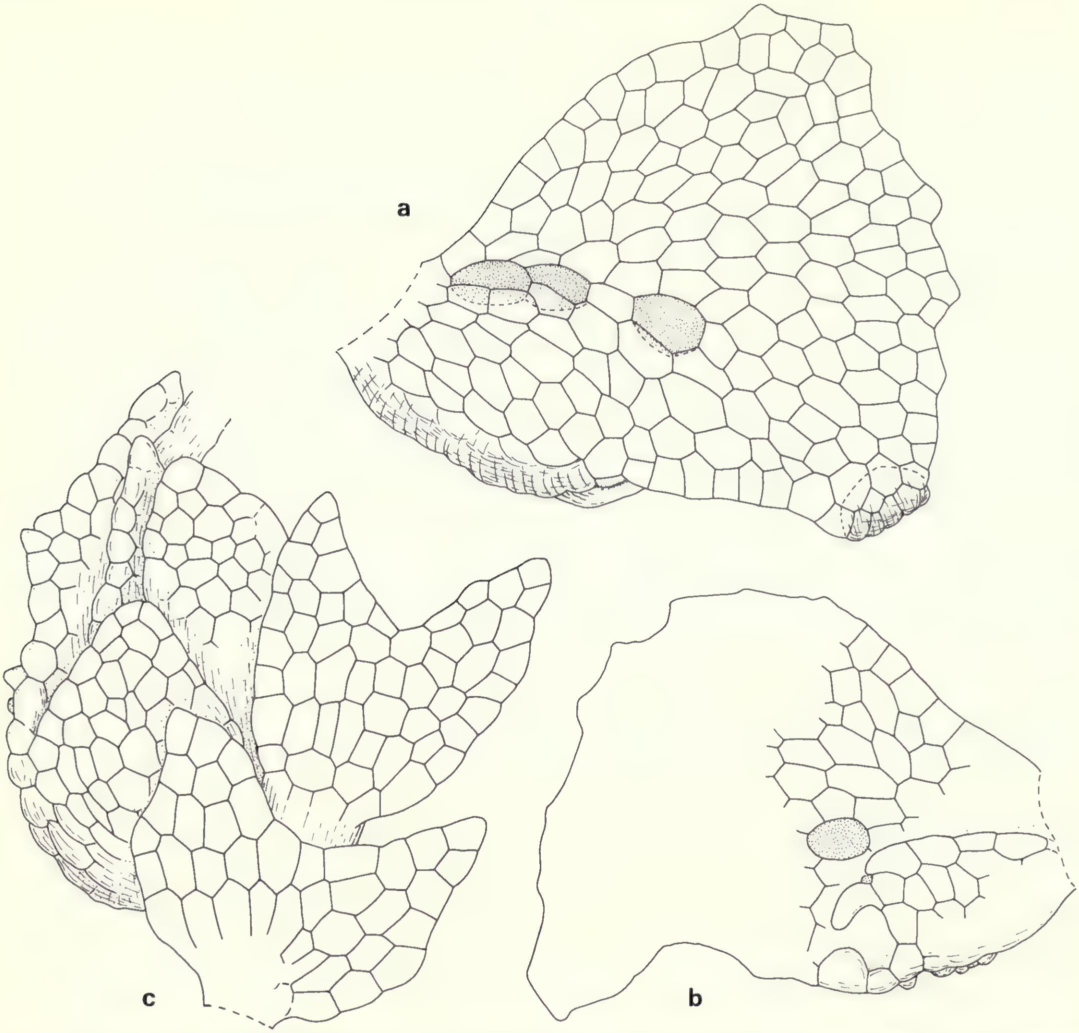

Fig. 5 *Drepanolejeunea ankasica* E. Jones. (a) leaf, antical view; (b) leaf, postical view; (c) part of male inflorescence showing two bracts with their underleaves. All ×280. Drawn from *Jones* 1377 (holotype) .

Cells of the antical margin of the lobe *c.* 15 × 15 μm, of the third and fourth rows in from the antical margin 20–25 × 15–22 μm, subapical cells 15–30 × 15–22 μm, median cells 24–36 × 15–18 μm, the walls thin with trigones small or absent, and weak intermediate thickenings; usually with three ocelli in an interrupted line, the two basal ocelli contiguous, just above the margin of the lobule, the upper ocellus isolated.

Underleaves two to two and a half times the width of the stem, obtrapeziform with widely diverging, broadly triangular lobes ending in a single short cell, separated by a very shallow broad sinus, the base cuneate.

Monoecious. Androecia on long or short shoots, often close to a gynoecium (sometimes on a subgynoecial innovation), of four or five pairs of bracts with large imbricate underleaves throughout, the bracts monandrous, antheridia 55–60 μm diam. Gynoecia often on short lateral shoots, sometimes on long shoots, with one or two subgynoecial innovations. Bracts and bracteole irregularly and bluntly dentate and containing ocelli. Perianth 0·33–0·35 × 0·4 –0·5 mm, obconic with five long deep equal keels and a strong rostrum; the keels more or less crenulate-dentate distally, especially on the angle, with conically protuberant cells.

GHANA. Ankasa River F.R., on twigs in the crown of a *Samanea* near the river, with *Colura* spp., *Diplasiolejeunea harpaphylla, Cheilolejeunea surrepens* etc., *Jones* 1377 p.p. (BM, holotype).

Drepanolejeunea ankasica belongs to the subgenus *Drepanolejeunea* Grolle (Grolle, 1976). In general appearance it resembles *D. claviformis* Stephani and *D. friesii* Vanden Berghen. It differs from both of these in being monoecious, in the slight development of trigones in the cells of the leaf, and in the apical tooth protruding far beyond its proximal neighbour; in *D. claviformis* and *D. friesii* the apical tooth is engaged for most of its length and free only near the apex. *Drepanolejeunea cultrella* (Mitten) Stephani is monoecious (though it has sometimes been described as dioecious), but has very different horned perianths and underleaves with narrow setiform lobes of elongate cells. *D. claviformis* also differs in its perianths (which are, however, usually rare) with their inflated obtuse horns.

2. **Drepanolejeunea cultrella** (Mitten) Stephani, *Sp. hepat.* **5**: 324 (1913); E. Jones in *Trans. Br. bryol. Soc.* **5**: 568 (1968).

SIERRA LEONE. Freetown Peninsula, three km north-east of Toke, epiphyllous, *Jones* s.n., depauperate and sterile, the determination therefore uncertain.

3. **Drepanolejeunea ?friesii** Vanden Berghen in *Svensk bot. Tidskr.* **45**: 366 (1951). Fig. 6.

SIERRA LEONE. Loma Mountains: on sheltered tree boles on margin of the forest near 'Camp 2', 1680 m (5500 ft), *Jones* 1474 p.p., 1475 p.p., 1477 p.p.; west of Bintimani, 1650 m (5400 ft), *Jones* 1491.

GHANA. Atewa Hills F.R., boughs in crown of *Cassipourea, Jones* 1299d; boughs in crown of *Lophira, Jones* 1319a; upper part of bole of *Antiaris, Jones* 1320b; mixed with other bryophytes on boles of trees in swamp forest, *Jones* 1331a p.p.

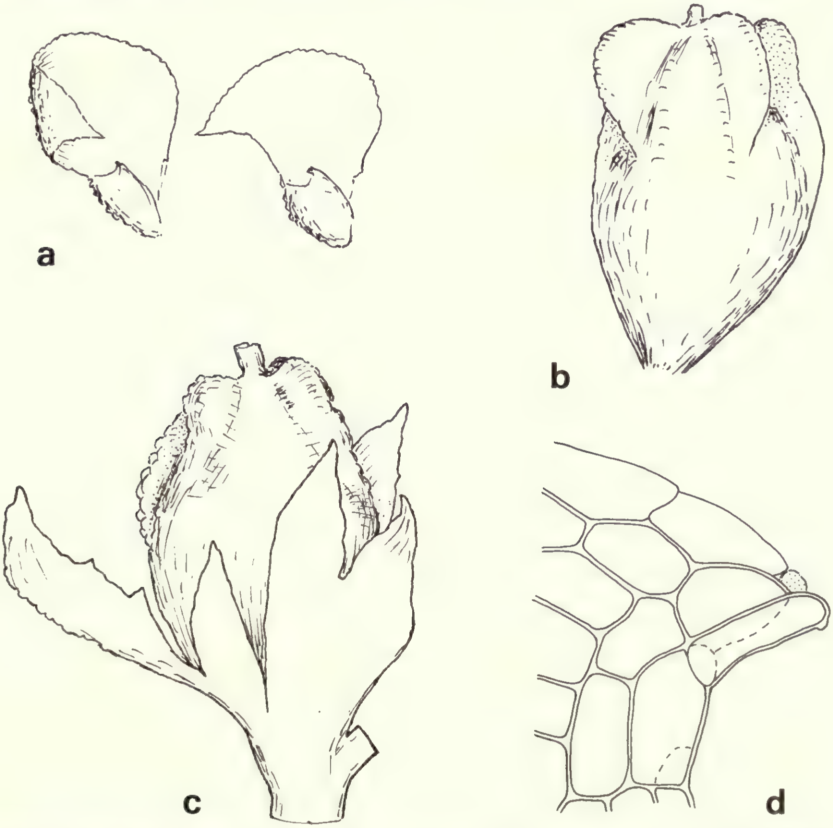

Fig. 6 *Drepanolejeunea ?friesii* Vanden Berghen. (a) leaves; (b) perianth; (c) perianth with involucre. All ×80. (d) apical tooth of lobule, ×666. Drawn from *Jones* 1320b.

Female inflorescences, but no perianths, are present in the collections from the Loma Mountains, but they appear to be the same as those from the Atewa Hills. Perianths (hitherto undescribed for *Drepanolejeunea friesii*) are present in *Jones* 1319a and, more copiously, in *Jones* 1320b.

Pearson (1931) recorded *Drepanolejeunea clavicornis* Stephani (= *D. claviformis* Stephani) amongst Saxby's collections from Tarkwa, Ghana, but it has not been possible to trace the specimen at either Manchester or Cambridge; it may have been the same species as that from the Atewa Hills. *D. friesii* is very similar to *D. claviformis* in vegetative characters; Vanden Berghen (1961) described them as differing chiefly in the absence of any basal ocellus from the leaves of *D. friesii* – an unusual feature in the genus. *D. claviformis* has been recorded only from West Africa, whereas *D. friesii* has been recorded from many localities in the East African mountains. The plants from the Loma Mountains and Atewa Hills, tentatively identified as *D. friesii,* have a line of two to three basal ocelli, sometimes interrupted, in some leaves, above the lobulus, but they are apparently not always present. The perianths are different from those described for *D. claviformis*, and the plants also seem to differ from *D. claviformis* and resemble *D. friesii* in the female bracts and bracteole which are almost entire, with only a few short coarse teeth – not laciniately dentate as in *D. claviformis.* The perianths of *Jones* 1320b are 0·6–0·7 mm long and 0·36–0·4 mm in diameter, inflated and terete proximally, contracted distally, with a strong rostrum and with five compressed equal keels in the upper half, the keels tuberculate with prominent cells.

XXV. DUMORTIERA Nees

1. **Dumortiera hirsuta** (Sw.) Nees in Reinw., Blume & Nees in *Nova Acta physico-med.* **12**: 410 (1824); Vanden Berghen in *Résult. scient. Explor. hydrobiol. Bassin Lac Bangweolo & Luapula* **8** (1): 182 (1972).

SIERRA LEONE. Loma Mountains, forest near 'Camp 1' above Sokurela, 1220 m (4000 ft), on stones and boulders partly submerged in stream, *Harrington* 269.

XXVI. FOSSOMBRONIA Raddi

1. **Fossombronia husnotii** Corbière in *Mém. Soc. natn. Sci. nat. Math. Cherbourg* **26**: 353 (1889); Vanden Berghen in *Résult. scient. Explor. hydrobiol. Bassin Lac Bangweolo & Luapula* **8** (1): 147 (1972).

SIERRA LEONE. Loma Mountains: Bintimani, 1890 m (6200 ft), on vertical rock face, *Jones* s.n.; also on west-facing cliffs of summit, on earth, *Harrington* 212 (without spores).

Fossombronia husnotii is widely distributed in tropical Africa, but is probably montane; it is, for example, known from the Uluguru Mountains in Tanzania (*Pócs* 6004/S, Herb Jones), and Jones collected a sterile plant which is probably this species on Mont Cameroun (Cameroon Mountain) at 2500 m (*Jones* 371). Its colourless rhizoids and the constant production of descending stolons and tubers form useful diagnostic characters. It is variable in size of spore and in the pattern formed by the lamellae on the face of the spore. Areolae may or may not be present in the centre of the face, but the lamellae are high, projecting as spines 5–10 μm tall around the periphery. In the plant from Bintimani the spores are 50–60 μm diam., without areolae, and with 20–24 spines.

2. **Fossombronia occidento-africana** S. Arnell in *Bot. Notiser* **105**: 317 (1952).

SIERRA LEONE. Freetown Peninsula: Mount Aureol ['Oriel'], *Arnell* 2413, 2448, 2517 (UPS), 2231, 2249, 2409 (S), 2497 (S, lectotype); Fourah Bay College, moist roadside bank, *Richards* R7086; Fourah Bay College B.R., on boulder by path to Heddle's Farm, *Harrington* 599; Charlotte Falls, shaded earth bank by road above the falls, *Harrington* 640 p.p. Musaia–Gbentu road, one mile north of the river Mongo, on bare earth in dried-up river bed, *Sellar* B35 p.p. Kambui Hills, Bambawo, shaded earth bank, *Harrington* 504. Giema, earth bank in roadside hollow, *Harrington* 555.

GHANA. Amedzofe, earth bank near the Training College, *Hall* (GC 47071); eroded earth below a land drain, *Hall* (GC 47226 & Herb. Jones). Konkori Scarp, Mole Game Reserve, abundant on sandstone rocks under trees, *Hall* s.n. – probably this species but without sporogonia.

Arnell described *Fossombronia occidento-africana* from his collections made on 'Mount Oriel' in 1951, but did not specify a type; 2497 is his most copious collection, with numerous mature sporangia, and it is one from which he made a microscope preparation; we therefore select it as the lectotype. The original description is inaccurate in certain respects. The following description is based on *Arnell* 2497 and on other collections from Sierra Leone and Ghana:

Monoecious, but probably protandrous. Shoots to *c.* 8 mm long, unbranched or occasionally dichotomous, not forming tubers. Stem in the fertile part of a shoot approximately semicircular in transverse section, 0·4–0·5 mm wide × 0·25–0·3 mm thick, in the older parts of the shoot narrower than thick, *c.* 0·2 × 0·25 mm; medullary cells with endophytic fungus. Rhizoids purple. Leaves more or less oblong or rounded-trapezoidal, slightly narrowed to the insertion, the apex truncate and retuse or rounded and very shallowly lobed, often undulate, 0·7–1·5 mm long × 0·75–1·5 mm wide. Cells of leaf near the apex 30 ×30–40 × 40 or 30 × 50 μm, in the middle of the leaf 25–45 × 35–60 μm, at the base up to 60 × 100 μm, the walls thin, without trigones, cuticle smooth.

Involucres obconic, *c.* 1·4 mm tall, the mouth irregularly lobed. Spores 36–50 μm diam. (40–45–50 μm in *Arnell* 2497), the distal face irregularly areolate, the areolae 4–6 μm diam., 8–10 across the face of the spore, the walls raised at the angles to form processes 2–3 μm tall which appear on the periphery of the spore as 30–40 or more 'spines'; the proximal face with only a few irregular thickenings. Elaters mostly 3-spiral, but many 2-spiral at one or both ends, and a few entirely 2-spiral. Cells of sporangium wall with massive radial thickened bands, very few of which extend across the tangential walls (thus not making 'semicircular' bands), 3–4 bands on each radial wall, spaced 10–15 μm apart in the undehisced sporangium, but more crowded after dehiscence.

Arnell described the cuticle as having '1–2 long striae per cell', and cells with 'sometimes small trigones'. We have not been able to find either striae or trigones, and they are certainly normally absent.

Fossombronia occidento-africana is the commonest species of *Fossombronia* in lowland West Africa; it is known from several localities in Nigeria (e.g. *Jones* 854 from Enugu) and is the plant that Augier (to whom we are indebted for lending us specimens) found at Yaoundé in Cameroon and which he assigned 'à titre provisoire' to *F. crozalsii* Corbière (Augier, 1972). We agree with Augier that this West African *Fossombronia* may indeed prove to be *F. crozalsii*, which is, however, imperfectly known. We have had to rely on descriptions and comparison with a single small specimen of *F. crozalsii* collected by Jones in Tubney Wood, Berkshire, England, in 1938. The chief differences seem to be:

(1) Spores of *Fossombronia crozalsii* are usually said to be not more than *c.* 40 μm diam. (e.g. Paton (1973) finds that they are 34–41 μm diam.), whereas spores of *F. occidento-africana* are often *c.* 45 μm or larger. But some collections have smaller spores; thus the plants from Amedzofe have spores 33–40 μm diam., and *Richards* R7086 from Fourah Bay College has spores 36–42 μm diam.

(2) The elaters are described as bispiral in *F. crozalsii*, though the Tubney Wood plant has some 3-spiral elaters.

(3) The Tubney Wood plant has much thinner and sparser bands of thickening in the sporangium wall.

Of these differences the last two seem to be the most important. We prefer to keep the two species separate until the range of variation of *F. crozalsii* is adequately known.

XXVII. **FRULLANIA** Raddi

1. **Frullania africana** Stephani in *Hedwigia* **30**: 269 (1891); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **46**: 151 (1976).

GHANA. Southern Scarp F.R., near Begoro, on *Celtis, Hall* s.n. (GC). Amedzofe, in coffee plantations, *Jones* s.n. (GC). Unlocalised and undated, *Akpabla* 588 (BM), the collecting number indicates that this was collected *c.* August 1936 in the Achimota district, possibly at Aburi (J. B. Hall, *in litt.*).

Not hitherto recorded from Ghana. Known only from a few scattered localities near the west coast of Africa, from the mouth of the Congo to Guinea. It appears to be characteristic of hill country, but occurs at lower altitudes than *Frullania arecae* which it resembles, except in its paroecious inflorescence and its 4- or 5-keeled perianth.

2. **Frullania apicalis** Mitten in *Phil. Trans. R. Soc.* **5**: 168 (1879); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **46**: 47 (1976), var. **apicalis**

SIERRA LEONE. Freetown Peninsula: Leicester Peak, on *Combretum* in scrub amongst rocks, 520 m (1700 ft), *Jones* 1453b; Sugar Loaf Mountain, *Richards* R7129, det. Vanden Berghen; three km north-east of Toke, on bole of small tree in thicket on rocky slope, *Jones* 1579, det. Vanden Berghen; Toke, on bole of large *Chrysobalanops* in thicket at the back of the beach, *Jones* 1445, det. Vanden Berghen; Picket Hill, on tree in forest just below the summit, *c.* 850 m (2800 ft), *Gledhill* s.n. Loma Mountains: between 'Camps 1 and 2', *c.* 1370 m (4500 ft), on rocks sheltered by trees, *Jones* 1472, det. Vanden Berghen; near 'Camp 2' (below Bintimani), 1520–1680 m (5000–5500 ft), on branch of isolated small tree, *Jones* 1480a, det. Vanden Berghen, and on adjacent rock, *Jones* 1480c, and on branches of *Craterispermum laurinum* on forest margin, *Harrington* 147, det. Vanden Berghen; *c.* three km south of 'Camp 2' between Bintimani and Dawule, 1370 m (4500 ft), on *Dissotis leonensis* growing amongst boulders, *Harrington* 229, det. Vanden Berghen. Gola Hills, Lalehun, on upper part of bole of large tree, *Jones* 1554a, det. Vanden Berghen.

GHANA. Ankasa River F.R., twigs in crown of *Samanea* by the Ankasa River rapids, *Jones* 1377 p.p. Atewa Hills F.R., *c.* 760 m (2500 ft), boughs in crown of *Braeya, Jones* 1286a, of *Lophira, Jones* 1319a, of *Antiaris, Jones* 1320, all det. Vanden Berghen; in crown of *Cassipourea, Richards & Hossain* (GC 36667).

Frullania apicalis has a wide, but disjunct, distribution in East Africa, where it is locally abundant from Uganda southwards to Mozambique, and in Madagascar and the Mascarenes. The distribution in West Africa is similarly disjunct, from the Bight of Biafra westwards to Sierra Leone. Usually its habitats seem to be montane, despite its occurrence at sea-level near Freetown. Thus, in Ghana it is abundant in the crowns of trees in the Atewa Hills, but was not found in the crowns of trees in the lowland forest reserve of Aiyaola. Its occurrence near sea-level in the Ankasa River Forest Reserve in western Ghana is paralleled by the presence of other montane species – e.g. *Radula boryana* and *Bazzania decrescens.* In the Freetown Peninsula *F. apicalis* is the only species of *Frullania* that has been recorded, and it appears to be rare. In the Loma Mountains it is abundant above *c.* 1400 m, together with lichens (e.g. *Usnea* sp., *Parmelia* spp., *Anaptychia* sp.) clothing the branchlets of isolated small trees and bushes that grow on rock outcrops.

Frullania apicalis grows on well-illuminated branches in the open crowns of large trees, or on isolated bushes and small trees. It appears to be restricted to natural communities.

3. **Frullania apiculata** (Reinw., Blume & Nees) Dumort., *Recueil observ. Jungerm.*: 13 (1835); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **46**: 102 (1976).

GHANA. Ankasa River F.R., twig in crown of *Samanea, Jones* 1377 p.p. Aiyinasi A.R.S., on branches of *Citrus, Jones* 1383, det. Vanden Berghen. Atewa Hills F.R., in crown of *Braeya, Jones* 1286c, det. Vanden Berghen; in crown of *Antiaris, Jones* 1320b.

Apparently a local species in Africa, in similar habitats to *Frullania apicalis,* with which it was mixed in *Jones* 1377, 1286, and 1320.

4. **Frullania arecae** (Sprengel) Gottsche in *K. dansk. Vidensk. Selsk. Skr.* **6**: 322 (1867); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **46**: 154 (1976).

Frullania ecklonii (Sprengel) Gottsche & Lindenb., *Syn. hepat.*: 413 (1845).

SIERRA LEONE. Lake Sonfon, on bole of mango at edge of forest, *Harrington* 26. Loma Mountains: *Jaeger* 1376 (PC), det. Vanden Berghen; near 'Camp 2', 1520 m (5000 ft), on branches of *Craterispermum laurinum* on edge of forest, *Harrington* 145 p.p., 146, det. Vanden Berghen.

GHANA. Aburi Botanical Gardens, on *Cupressus, Jones* s.n. (GC).

5. Frullania depressa Mitten in *J. Proc. Linn. Soc.* **7**: 168 (1863 ['1864']); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **46**: 206 (1976).

SIERRA LEONE. Loma Mountains: near 'Camp 2', 1520–1680 m (5000–5500 ft), on branches of small isolated trees, *Jones* 1480b, 1495 p.p., 1497b; Bintimani, on dolerite rocks at foot of west-facing cliffs, *c.* 1830 m (6000 ft), *Harrington* 221, det. Vanden Berghen.

On the Loma Mountains usually associated with *Frullania apicalis*. A local montane species known elsewhere in Africa from Cameroon and in widely scattered localities in East Africa, from Ethiopia southwards to Zimbabwe, and in Madagascar.

6. Frullania diptera (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees, *Syn. hepat.*: 420 (1845); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **46**: 194 (1976).

GHANA. Bunso, on cocoa, *Jones* s.n. Kpedze Rest House, on cocoa, *Jones* s.n. Between Bame and Todome, on cocoa, *Jones* s.n.

A local and apparently rather rare species, which apparently always occurs in small quantities, not hitherto recorded from Ghana. The records cited by Vanden Berghen (*op. cit.*) show three main areas where it occurs: (1) the lower hills in south-eastern Kenya and north-eastern Tanzania, from the Shimba Hills to the Southern Highlands, (2) central Madagascar, (3) the coastal region of South Africa, from Capetown to Durban. For West Africa he gives only a single record, from northern Nigeria. It may, however, be much overlooked, as it is not conspicuous and rarely, if ever, occurs abundantly in pure patches. It is pale, often yellowish green in colour, with flat complanate leaves closely appressed to the substratum. Although it occurs as high as 1750 m in Tanzania, it seems to be chiefly a lowland species.

7. Frullania eplicata Stephani, *Sp. hepat.* **4**: 679 (1911); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **46**: 83 (1976).

GHANA. Aiyaola F.R., on boughs of *Piptadeniastrum, Jones* 1233, det. Vanden Berghen. Amedzofe, in savanna woodland just below the summit of the hill, on the upper part of the boles of old but small *Lophira* and *Terminalia, Jones* 1258, det. Vanden Berghen.

8. Frullania ericoides (Nees) Montagne in *Annls Sci. nat.* (Bot.) II, **12**: 51 (1839); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **46**: 161 (1976).

Frullania squarrosa (Reinw., Blume & Nees) Dumort., *Recueil observ. Jungerm.*: 13 (1835).

SIERRA LEONE. Musaia town, on mango, *Donald* s.n. Kabala, on tree trunk in open woodland below the District Officer's bungalow, *Harrington* 137 p.p. About four km south of Kabala, on isolated small tree in swampy valley, *Harrington* 118 p.p. About five km south of Kabala, on small tree in secondary forest, *Harrington* 125 p.p. Lake Sonfon, on tree trunk at edge of forest surrounding the 'lake', *Harrington* 27. Loma Mountains, Seradu, on tree boles in forest by the village, in small amounts mixed with *Mastigolejeunea auriculata* etc., *Jones* 1515, 1517.

GHANA. Bia North F.R., boughs in crown of *Entandophragma* etc., rare, *Jones* ! Asenanyo F.R., in crown of *Triplochiton, Jones* 1412 p.p., det. Vanden Bergen. Kumasi, in garden, *Irvine* 17. Oda, on cocoa, *Irvine* 10. Southern Scarp F.R., near Begoro, *Jones* ! Aburi Botanical Gardens, *Foote* 3, *Irvine* 19a, *Jones* s.n. Amedzofe, abundant in farms, *Jones* ! Between Bame and Todome, on cocoa, *Jones* s.n.

Pantropical and polymorphic, *Frullania ericoides* is probably the most abundant species of its genus, predominantly lowland (though ascending to 2000 m in East Africa), and extending through a wide range of rainfall regimes. It is particularly frequent in farmland, secondary forest, and similar disturbed sites. The above records do not adequately indicate its abundance in southern Ghana, as, despite it polymorphism, it is easily recognized in the field and therefore need not be collected. On the other hand the indications of its rarity or absence from southern and western Sierra Leone are probably genuine. It is remarkable that it has not been recorded from around Freetown, where apparently suitable disturbed habitats abound, nor from Njala.

9. Frullania nodulosa (Reinw., Blume & Nees) Nees, *Syn. hepat.*: 433 (1845); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **46**: 132 (1976).

SIERRA LEONE. Gola North F.R., on fallen bough, *Jones* 1571 p.p.
GHANA. Subri F.R., on fallen bough, *Jones* 1353. Oda, on cocoa, *Irvine* 9a. Kade A.R.S., crown of *Parinari, Hossain* (GC 36700). Aiyaola F.R. near Kade, crown of *Triplochiton, Jones* 1227b (GC). Also unlocalised specimens – *Burton & Cameron* s.n. (BM) and *Cummins* s.n. (BM).

Apparently confined to the crowns of trees in old natural forest, and therefore most frequently seen on fallen boughs.

10. Frullania obscurifolia Mitten in *Phil. Trans. R. Soc.* **5**: 168 (1879); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **46**: 143 (1976).

Frullania borgenii Pearson in *Forh. VidenskSelsk. Krist.* **1890** (2): 8 (1891).

SIERRA LEONE. Kabala, on tree-bole in open woodland below the District Officer's bungalow, *Harrington* 136 p.p., det. Vanden Berghen.
GHANA. Aburi Botanical Gardens, on palm, *Jones* 1577, det. Vanden Berghen.

11. Frullania purpurea Stephani, *Sp. hepat.* **4**: 626 (1911); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **46**: 77 (1976).

SIERRA LEONE. Kasabere Hills, on small savanna tree, *Richards* (*Jones* 1580), det. Vanden Berghen. Kasewe F.R., on small savanna tree, *Richards* s.n. (Herb. Jones). The two localities are very close together.

A rare species, known elsewhere only from Benin (*Jones* 148), Calabar (*Jones* 211 p.p.), and, according to Vanden Berghen (*op. cit.*), São Tomé (*Moller* 20), Madagascar (five records), and Mauritius (two records).

12. Frullania spongiosa Stephani in *Hedwigia* **33**: 147 (1894); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **46**: 167 (1976).

GHANA. Bia North F.R., boughs in crown of *Entandophragma, Jones* 1411 p.p., det. Vanden Berghen. Krokosua Hills, on cocoa in farms near Bia bridge, *Jones* 1388a, det. Vanden Berghen. Asenanyo F.R., bough in crown of *Triplochiton, Jones* 1412, and of *Terminalia superba, Jones* 1413, det. Vanden Berghen. Oda, *Irvine* 7, and on cocoa, *Irvine* 9b, 10. Bunso, on base of oil palm, *Jones* 1301, det. Vanden Berghen. Kade A.R.S., upper branches of *Aningeria, Hossain* (GC 39321, 39325, 39335). Osenasi, on cocoa, *Jones* s.n. Aburi Botanical Gardens, on palm trunks, *Irvine* 22; on *Cupressus, Jones* s.n., det. Vanden Berghen; *Jones* 1576, det. Vanden Berghen. Amedzofe, 730 m (2400 ft), abundant on cocoa in farms above the waterfall, *Jones* 1270, det. Vanden Berghen. Vane, on rocks in roadside banks, *Jones* 1266b, det. Vanden Berghen.

Perhaps the most abundant species of *Frullania* throughout much of southern Ghana, and like *F. ericoides* to which it is allied, especially frequent in farms on planted cocoa, etc., but also found in the crowns of large trees in natural forest. It is similarly abundant in parts of southern Nigeria and Cameroon, and like several other species of *Frullania* seems to occur in a disjunct area in East Africa.

13. Frullania trinervis (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees, *Syn. hepat.*: 427 (1845); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **46**: 198 (1976).

SIERRA LEONE. Kabala, on tree trunk in open woodland below the District Officer's bungalow, *Harrington* 137.
GHANA. Between Bame and Todome, on cocoa, *Jones* s.n.

Widely distributed throughout tropical and South Africa. From analogy with Nigeria it may be expected to have its greatest frequency in northern Ghana and Sierra Leone; Vanden Berghen (*op. cit.*) cites records from that part of Guinea between Sierra Leone and the headwaters of the Senegal River.

XXVIII. **GONGYLANTHUS** Nees

1. **Gongylanthus ericetorum** (Raddi) Nees, *Naturgesch. europ. Leberm.* **2**: 407 (1836); E. Jones in *Trans. Br. bryol. Soc.* **4**: 649 (1964); Vanden Berghen in *Résult. scient. Explor. hydrobiol. Bassin Lac Bangweolo & Luapula* **8** (1): 45 (1972).

SIERRA LEONE. Loma Mountains, frequent on earth amongst grass tussocks from *c.* 1220 m (4000 ft) upwards: south of 'Camp 2', *Harrington* 296 p.p.; near 'Camp 2', 1520 m (5000 ft), *Harrington* 144; lower slopes of Bintimani Peak, on peaty soil, 1680 m (5500 ft), *Harrington* 178.

2. **Gongylanthus richardsii** E. Jones in *Trans. Br. bryol. Soc.* **4**: 650 (1964).

SIERRA LEONE. Loma Mountains, frequent on Bintimani, but generally at higher levels than *Gongylanthus ericetorum*, not descending below *c.* 1830 m (6000 ft): summit plateau, beneath overhanging rock, *c.* 1940 m (6360 ft) *Harrington* 208; on earth around tussocks of *Trilepis, Hypoxis* etc., 1860–1900 m, *Jones* 1487.

Known elsewhere only from the volcanic soils of Mont Cameroun (Cameroon Mountain) and, in Tanzania, of Kilimanjaro (Bizot & Pócs, 1974) and Rungwe.

XXIX. **JUNGERMANNIA** L.

1. **Jungermannia ?borgenii** Gottsche ex Pearson in *Forh. VidenskSelsk. Krist.* **1892** (14): 11 (1893); Váňa in *Folia geobot. phytotax.* **9**: 289 (1974).

SIERRA LEONE. Musaia–Gbentu road, one mile north of the river Mongo, on bare earth in dried-up river bed, *Sellar* B35 p.p. (no perianths seen). Musaia Agricultural Station, on bare ground near the Rest House, *Sellar* B12 p.p. (no perianths seen).

Jungermannia borgenii is widely distributed in tropical Africa and extends to South Africa and the Mascarenes.

I am sceptical as to whether *Jungermannia borgenii* can be safely separated from *J. dusenii* (Stephani) Stephani in the absence of perianths. [E.W.J.]

XXX. **LEJEUNEA** Libert

1. **Lejeunea autoica** R. M. Schuster in *J. Hattori bot. Lab.* **25**: 6 (1962); E. Jones in *J. Bryol.* **10**: 389 (1979).

GHANA. Atewa Hills F.R., *c.* 730 m, on boughs in crown of *Braeya, Jones* 1286 p.p.; on bole of middle-storey tree, *Jones* 1291; on stem of *Vernonia, Jones* s.n.

Originally described from Florida, and recorded elsewhere only from the Atewa Hills and Mont Cameroun (Cameroon Mountain), this imperfectly known species is likely to prove widely distributed. It could readily be passed over as the much more abundant dioecious species, *Lejeunea confusa*.

2. **Lejeunea brenanii** E. Jones in *J. Bryol.* **10**: 391 (1979).

SIERRA LEONE. Freetown Peninsula: Leicester Peak, in low forest just below the summit, *Brenan* (*Jones* 463, 464); on twigs and stems of shrublets amongst rock outcrops, 520 m (1700 ft), *Jones* 1455; on twigs of *Phyllanthus* in open scrub, 520 m, *Jones* 1457b. Gola North F.R., on upper part of bole of large tree, *Jones* 1554b.

GHANA. Krokosua Hills F.R., abundant on boughs in the crowns of trees, 520–550 m (1700–1800 ft), *Jones* 1398; on exposed stems of shrubs on edge of forest, *c.* 550 m, *Jones* 1401a; epiphyllous on *Culcasia, Jones* 1399 p.p. Atewa Hills F.R., in crown of *Cassipourea* in small amounts on the sides of boughs and in crooks, where few other plants are present, *Jones* 1298. Aburi Botanical Gardens, *Irvine* s.n., *Foote* 4, *Jones* s.n. Amedzofe, near the waterfall, *Irvine* 412.

Lejeunea brenanii is one of a group of critical taxa allied to *L. flava*, distinguished from the other members by its large size, large cordate underleaves, dioeciousness, long androecia with underleaves throughout, narrowly but longly keeled perianths, etc. It is evidently locally abundant and somewhat montane, often clothing the well-illuminated branchlets of trees and bushes with a mantle of long pendent shoots. When sterile it would be indistinguishable from *L. ramosissima*. J. Augier (*in litt.*) has recently detected it amongst his collections from Cameroon.

3. Lejeunea caespitosa Lindenb., *Syn. hepat.*: 382 (1845); E. Jones in *J. Bryol.* **7**: 37 (1972).

SIERRA LEONE. Freetown Peninsula: Mount Aureol ['Oriel'], *Arnell* 2334b (Herb. Jones); boles of small trees by Mountain Torrent, *Jones* 1443, also s.n. Bo, near the school, epiphyllous, *Revell* (Herb. Jones). Loma Mountains, above Seradu, epiphyllous, 1040 m (3400 ft), *Jones* s.n. Kambui Hills, Bambawo, on bole of *Musanga, Jones* 1534; on mango leaves near the ground, *Jones* 1541b. Gola North F.R., epiphyllous by stream in forest, *Jones* 1567 p.p.

GHANA. Aiyinasi A.R.S., on *Citrus, Jones* 1363b. Asanta, abundant on coconut palms on the beach, *Jones* 1359c. Asenanyo F.R., on boughs in crown of *Triplochiton* etc., *Jones* 1412; buttress of *Terminalia, Jones* s.n. Pra-Suhien F.R., rotting log in deep shade, *Jones* 1344a; epiphyllous, *Jones* 1345c p.p. Bobiri F.R. (6°39′ to 6°42′N, 1°16′ to 1°23′W), rotting log in deep shade, *Jones* 1414. Ochi Headwaters F.R., *West-Skinn* 147, 153. Kade A.R.S., bole of *Parinari, Hossain* (GC 36686); bole of *Diospyros, Jones* 1223. Aiyaola F.R. near Kade, in crown of *Triplochiton*, *Jones* 1227c, 1229; on liane, *Jones* 1241. Atewa Hills F.R., on bole of *Cassipourea, Richards & Hossain* (GC 36685); epiphyllous on low herbs at edge of small gap in forest, *Jones* 1294 p.p. Begoro, rocks in dry stream bed below the waterfall, *Jones* 1307b p.p. Begoro–Bunso road, on buttress of *Celtis, Jones* 1303. Bunso, on boles of cocoa, *Jones* 1317a. Aburi Botanical Gardens, on bough of *Cupressus, Jones* s.n. Amedzofe, on shade trees in coffee farm, *Jones* 1247; on bole of old *Combretum* in savanna woodland just below summit of the hill, *Jones* 1259b; on rocks by stream just above the waterfall, *Jones* 1277; epiphyllous by the stream in cocoa farms, *Jones* 1273. Kpedze Rest House, on cocoa, *Jones* s.n.

One of the commonest species of *Lejeunea* in lowland habitats throughout the wetter parts of tropical Africa, and possibly pantropical, having been recorded from other countries under other names; polymorphic. It is most commonly corticolous or lignicolous in shady, sheltered places. As the above records show, it sometimes grows in the crowns of large forest trees, but is much rarer here than on tree boles near the ground.

In many districts it does not occur as an epiphyll, or does so only exceptionally, but in some localities in Ghana and Sierra Leone it was abundant on leaves. The epiphyllous forms tend to have underleaves which are conspicuously lunate, being deeply divided into narrow lobes which are often only 2–3 cells wide at the base, and the cells 2–3 times as long as wide, thus resembling the American *Lejeunea longifissa* Stephani (regarded as conspecific by Schuster (1980)). Such plants may look distinctive, but the underleaves vary greatly, and often undergo transitions within a single shoot to the broader-lobed, short-celled form which is commonest in other habitats.

4. Lejeunea camerunensis (Stephani) E. Jones in *J. Bryol.* **7**: 33 (August 1972) [non *L. kamerunensis* (Stephani) Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **42**: 446 (December 1972)].

Eulejeunea camerunensis Stephani, *Sp. hepat.* **6**: 417 (1923) (see Art. 68.1).
Lejeunea tuberculiflora E. Jones ex Pócs in *Acta bot. hung.* **25**: 231 (1979), nom. illeg. (Art. 63.1).
? *Eulejeunea microclada* Pearson in *Annls Cryptog. exot.* **4**: 66 (1931).

SIERRA LEONE. Freetown Peninsula: Mount Aureol, *c. per., Arnell* 2334a (S, as *Lejeunea saccatiloba* Stephani); Fourah Bay College B.R., on bole of tree near Heddle's Farm, *c. per., Jones* 1421; Leicester Peak, on old mango, sterile, *Jones* 1464 p.p.; Toke, on old *Terminalia scutifera* on the beach, male, *Jones* 1444a. Kabala, on trunk of mango near the District Officer's bungalow, *c. per., Harrington* 140 p.p. Between Sokurela and Kurubonla, *c.* 500 m, on bole of *Uapaca, c. per., Jones* 1522c. Loma Mountains: forest above Sokurela, 910–1220 m (3000–4000 ft), on tree bole, mixed with *Porella subdentata, Plagiochila* spp. & *Lejeunea eckloniana, c. per., Jones* 1467b; Bintimani Peak, *c.* 1830 m (6000 ft), amongst dolerite boulders, *c. per., Harrington* 203 p.p. Kambui Hills, Bambawo, on boles of small trees in moderate shade, in forest above the old mine, *c. per., Jones* 1531, 1535; on old mango bole by the staff bungalows, *c. per., Jones* 1549. Jawo, near Kenema, by the river Moa, on tree boles at or just above the top of the flood zone, mixed with *Lejeunea setacea, c. per., Jones* 1536b. Gola Hills, Lalehun, shaded bole of tree, *c. per., Jones* 1556.

GHANA. ? Ankasa River F.R., in crown of *Glutea,* sterile, *Jones* 1378 p.p. ? Tafo Cocoa Research Inst., on trees in garden, sterile, *Jones* s.n. ? Bunso, on cocoa, female but without perianths, *Jones* 1317a. Kade A.R.S., on upper branches of *Aningeria robusta,* male, *Hossain* (GC 39330); female, but without perianths, *Hossain* (GC 39331); on bole of *Parinari excelsa,* male, *Hossain* (GC 36689). Amedzofe, on bole of old shade-tree in coffee farm, *c. per., Jones* 1245; in savanna woodland just below summit of the hill, on bole of *Combretum, c. per., Jones* 1256, and on *Terminalia,* male, *Jones* 1257c.

Lejeunea camerunensis is widely distributed and often abundant in the wetter parts of tropical Africa, extending eastwards to Mauritius. In the absence of the characteristic perianths, however, it cannot be identified with certainty; thus records based on male or sterile plants must be regarded as doubtful. Jones (*op. cit.*) described the apical tooth of the lobule as 'up to twice as long as wide', and the perianth as 'ecarinate, terete or bluntly angled at the sides and ventrally in the upper half, dorsally plane'. Some of the plants from eastern Sierra Leone (*Jones* 1531, 1556) show considerable variation in the perianths, some of which are weakly carinate near the apex, and may have a weak dorsal keel, though they have the characteristic tuberculate cells. *Jones* 1535 has completely ecarinate perianths, whereas *Jones* 1531 from the same site has perianths that are distinctly carinate. The apical teeth of the lobules of these plants are also somewhat longer than previously described – up to 30 × 10 μm.

The type of *Eulejeunea microclada* Pearson has not been found; Pearson described only male inflorescences. What is presumably the same species exists mixed with Saxby's specimen of *Cheilolejeunea newtonii* at CGE, but is sterile. The synonymy of *E. microclada* with *Lejeunea camerunensis* thus remains uncertain.

5. Lejeunea confusa E. Jones in *J. Bryol.* **7**: 24 (1972).

Microlejeunea jungneri Stephani, *Sp. hepat.* **5**: 812 (1915), non *Lejeunea jungneri* Stephani (1896).

SIERRA LEONE. Freetown Peninsula, on stems of bushes by Mountain Torrent, mixed with *Lejeunea caespitosa, Cheilolejeunea serpentina* et al., *c. per., Jones* 1443b. Lake Sonfon, on small tree in grassland near the 'lake', *Harrington* 31 p.p. Loma Mountains, Bintimani Peak, 1830 m (6000 ft), amongst dolerite boulders, *Harrington* 203 p.p. Kambui Hills, Bambawo, epiphyllous on low vegetation near pool in forest, *Harrington* s.n.; epiphyllous on low vegetation near stream, *Harrington* 423 p.p. Gola North F.R., on bole of *Vitex* mixed with *Calymperes* sp., *c. per., Jones* 1558.

GHANA. Ankasa River F.R., on bole of *Vitex, Jones* 1369, and in the crown, *Jones* 1368b.

Widely distributed and frequently abundant in tropical Africa, extending eastwards to Tanzania, but difficult to identify when sterile. Perianths are usually rare and difficult to find. It may readily be confused with small forms of *Lejeunea caespitosa* or with *L. autoica*, both of which differ in being monoecious and in the structure of the well-developed lobulus; *L. caespitosa* also has larger cells and a more translucent texture. *L. confusa* is usually corticolous; its exceptional occurrence as an epiphyllous species in Sierra Leone parallels the exceptional occurrence there of *L. caespitosa* and *Cheilolejeunea serpentina* as epiphylls.

6. Lejeunea eckloniana Lindenb., *Syn. hepat.*: 381 (1845); E. Jones in *J. Bryol.* **8**: 78 (1974).

SIERRA LEONE. Freetown Peninsula: Leicester Peak, 520 m (1700 ft), on rock, sheltered by deciduous bushes, *Jones* 1456; valley above Kongo Dam, Bathurst, 490 m (1600 ft), on barkless rotten log in forest, *Jones* 1434b p.p.; Guma Valley, on trunk of small tree in forest, *Harrington* 109. Loma Mountains: Sokurela, 610 m (2000 ft), on bole of oil palm in swamp forest, *Jones* 1465a; between Sokurela and 'Camp 1', *Harrington* 394, 395, *Jones* 1467c; forest above Sokurela, 1220 m (4000 ft), on boulder, *Jones* 1470 p.p. Kambui Hills, Bambawo, epiphyllous on low vegetation by stream in forest, *Harrington* 423 p.p.; on boles of small trees in forest, 340 m (1100 ft), *Jones* 1527 p.p., 400 m (1300 ft), *Jones* 1547b.

GHANA. Krokosua Hills, 550 m (1800 ft), on well-illuminated but sheltered stems of shrubs on edge of forest (sterile and elobulate), *Jones* 1401a p.p. Afram Headwaters F.R., on log in fragment of natural forest, *Jones* s.n. Subri F.R., on decaying *Raphia* palm in swamp forest, *Jones* 1352. Begoro, in dry stream bed below the waterfall, *Jones* 1307b; on flat rocks just above water level by the stream above the falls, *Jones* 1311 p.p. Atewa Hills F.R., on stem of *Vernonia, Jones* s.n. Kade A.R.S., on boles of small trees in forest, *Jones* 1216b, 1223. Aiyaola F.R. near Kade, bole of small tree, *Jones* 1231; on liane, *Jones* 1241. Aburi Botanical Gardens, frequent, *Jones* s.n. Amedzofe, on old *Combretum* in savanna woodland just below summit of the hill, *Jones* 1259; on wet rocks in stream just above the waterfall, *Jones* 1278b;

epiphyllous, abundant, mixed with *Taxilejeunea conformis,* on tall herbs beneath dripping cliffs in ravine above the waterfall, *Jones* 1285b. Kpedze Rest House, on cocoa, *Jones* s.n. Between Todome and Bame, on cocoa, *Jones* s.n.

Widely distributed, variable, and often abundant, *Lejeunea eckloniana* is difficult to separate in the field from other medium-sized species of *Lejeunea,* but microscopic examination of fresh living plants will show the distinctive simple oil-bodies. The variation and difficulties of determination are discussed by Jones (*op. cit.*); it is possible that more than one taxon is included. *Jones* 1456 from Leicester Peak is a remarkable robust form, in which all the perianths are borne on short lateral branches which lack subgynoecial innovations; a similar plant (*Jones* 1470 p.p.) was gathered in the Loma Mountains. If these plants were examined alone they would be ascribed to a different species or even (if the absence of subgynoecial innovations was considered to be a generic character) to a different genus. Intermediate conditions exist, however, and *L. eckloniana* shows a strong tendency to produce some gynoecia without, or with reduced, innovations.

7. **Lejeunea flava** (Sw.) Nees, *Naturgesch. europ. Leberm.* **3**: 277 (1838); E. Jones in *Trans. Br. bryol. Soc.* **5**: 548 (1968), subsp. **flava**

SIERRA LEONE. Freetown Peninsula: Havelock Plateau, bole of small tree in scrub, *Jones* s.n.; Leicester Peak, 490–595 m (1600–1950 ft), abundant on boles of small trees and on twigs of bushes both in deep shade and in open scrub in rocky ground, *Brenan* (*Jones* 462), *Jones* 1429, 1430, 1457, 1462d; forest in valley above Bathurst, *c.* 430 m (1400 ft), on tree bole, *Jones* 1437. Loma Mountains, valley-head west of Bintimani, 1680 m (5500 ft), under bushes in deep shade, with *Taxilejeunea conformis, Jones* 1498b.

GHANA. Kade A.R.S., on smooth well-lit tree bole in natural forest, *Jones* 1220. Aiyaola F.R. near Kade, side of main bough in crown of *Khaya, Jones* 1238.

See the discussion on the taxonomic treatment of *Lejeunea flava* following *L. grossecristata.*

8. **Lejeunea grossecristata** (Stephani) E. Jones in *Trans. Br. bryol. Soc.* **5**: 556 (1968).

Taxilejeunea nicholsonii Pearson in *Annls Cryptog. exot.* **4**: 64 (1931).

SIERRA LEONE. Lake Sonfon, on edge of forest surrounding the 'lake', on mango, *Harrington* 24 p.p., 25 p.p., on small tree, *Harrington* 41. Bo, on dead tree stump, *Gardner* 130 p.p.

GHANA. Krokosua Hills F.R., 550 m (1800 ft), on exposed stems of pioneer shrubs on margin of forest, *Jones* 1401b. Atewa Hills F.R., bough in crown of *Cassipourea, Jones* 1322 p.p. Bunso, on cocoa, *Jones* 1317a. Tafo, on bole of isolated tree in garden, *Jones* 1333. Aburi Botanical Gardens, on roots of epiphyte on palm, and on tree bole, *Jones* s.n. Amedzofe, in savanna woodland just below summit of the hill, on boles of old *Lophira* and *Terminalia, Jones* 1257a, b, c, e; on cocoa in farms just above the waterfall, *Jones* 1272b.

The complex of autoecious plants included under, or closely allied with, *Lejeunea flava* is a taxonomically difficult group. Jones (*op. cit.*) tentatively recognized in Africa *L. flava* subsp. *flava, L. flava* subsp. *tabularis* (Sprengel) S. Arnell, *L. longirostris* (Stephani) E. Jones, and *L. grossecristata,* though he expressed doubts as to the distinctness of the last three, and in 1979 he accepted *L. longirostris* as synonymous with *L. grossecristata.* While collecting in 1971 he paid particular attention to this group. The plants from Sierra Leone and Ghana seem to fall into two groups:

(1) Lax, often elongate plants with leaves distant or approximate, the underleaves small (0·26–0·36 mm wide), a quarter to a third the width of the shoot, distant to approximate, ovate or cordate-ovate, the perianths small, up to *c.* 0·56 mm long, keeled in the upper third or half, usually with one subgynoecial innovation.

(2) Shorter plants, often closely applied to bark, with leaves approximate to imbricate, underleaves large (0·3–0·45 mm wide), a third to a half the width of the shoot, rounder than those of (1), thus circular rather than ovate, and more strongly cordate at the base, imbricate at least below female inflorescences, perianths larger, 0·6–0·7 mm long, the keels longer and deeper than in (1), extending below the middle of the perianth, often with two subgynoecial innovations.

Weak shoots of group (2), and the basal portions of branches, often have small distant underleaves. It is arguable that the two groups represent hygromorphic and xeromorphic, or perhaps shade- and light-forms, of a single taxon, but on the whole the field evidence suggests that they are different. The fact that the two groups seem to have different geographical distributions supports this belief. Group (1) corresponds with *Lejeunea flava* subsp. *flava*; the other group can be assigned either to subsp. *tabularis* or to *L. grossecristata*, if indeed these two are different taxa. In their tendency to be closely applied to bark, and to have imbricate leaves accrescent to the female inflorescence, they differ from subsp. *tabularis* as it occurs in South Africa, and are clearly the same as *Jones* 212 from Calabar, Nigeria, which was considered to be *L. grossecristata* by Jones (1968*a*). A satisfactory taxonomic treatment of this complex can probably only be attained after a much fuller study of the variation within and between populations than has yet been undertaken, combined with experimental work.

It has not been possible to trace the holotype specimen of *Taxilejeunea nicholsonii* Pearson at MANCH; it was collected at Tarkwa, Ghana, by Saxby. Pearson (*op. cit.*) described it as autoecious, with perianths 'narrowly obovate, 5-angled, slightly winged, rostellate', and androecia 'sessile . . .; 2–4 pairs of bracts'; perianths were said to be abundant. A packet at CGE contains copious material but is nearly sterile, with only a few poor androecia, suggesting that the plant might be dioecious. Assuming that the CGE packet represents the same plant as the type, and that Pearson's observations are correct (as, indeed, they are likely to be) *T. nicholsonii* should be regarded as a synonym of *Lejeunea grossecristata.* A 'Taxilejeuneoid' female inflorescence would conform with this identification.

9. Lejeunea ibadana A. Harrington & E. Jones in *J. Bryol.* **12**: 40 (1982).

? *Lejeunea corbieri* Stephani in *Bull. Mus. natn. Hist. nat. Paris* **18**: 119 (1912).

SIERRA LEONE. Kambui Hills, Bambawo, 370 m (1200 ft), on rotting log in forest, *Jones* 1548.

GHANA. Pra-Suhien F.R., on rotting log in deep shade, *Jones* 1344c. Kade A.R.S., on base of large liane in deep shade in forest, *Jones* 1219 p.p. Amedzofe, on bole of cocoa in farms above the waterfall, *Jones* 1272a.

Lejeunea ibadana is widely distributed and locally abundant in West Africa, especially on decaying vegetable matter such as rotting logs and bases of oil palms. It is present in Stephani's herbarium (G 1173 from Bouroukrou, Ivory Coast) as ? *L. corbieri.* The type of *L. corbieri,* from Bangui, Central African Republic, consists mostly of *L. setacea* Stephani, but includes a small admixture of a *Lejeunea* which *may* be *L. ibadana,* but which is too scanty and imperfect for a safe determination. Unfortunately, Stephani's original description is not adequate to indicate whether his *L. corbieri* is the plant that we have described as *L. ibadana.*

10. Lejeunea lomana E. Jones, **sp. nov.** Fig. 7.

Surculi cum foliis c. 1 mm lati, caule 90 μm diam., appressi, irregulariter ramosi. Folia complanata, approximata vel leviter imbricata, c. 0·5 × 0·4 mm, ovalia vel ovata, apice rotundata; lobulus magnus, lobo triplo brevior, oblongus, basin et carinam versus inflatus, apicem versus compressus; carina leviter arcuata, cum margine lobi postico sinus latum et non profundum delimitans; margo lobuli liber ex 6 cellulis constructus; dens apicalis substrictus, c. 40 μm longus × 13 μm latus, apice solum liber, praeterea ad marginem lobuli apicalem conjunctus; papilla hyalina ex apice dentis lateraliter oriens et marginem librum contingens. Amphigastria orbicularia, ad medium bifida, quam caule 1½–2-plo latiora. Cellulae lobi medianae 18–24 × 24–35 μm, leptodermatae, trigonis parvis aut mediocris sed manifestis, incrassationibus intermediis nullis.

Dioica. Androecia vulgo 6–7 jugae, in ramis longis intercalata. Perianthia 0·5–0·8 × 0·33–0·5 mm, teretia, pyriformia, circum apicem 5-carinata, carinis non altis, consimilibus. Bracteae femineae perianthio paulo breviores, obovatae, lobulis lobo 1½-plo brevioribus, carinis aut bractearum superiorum aut bractearum ambarum leviter alatis.

Typus: *E. W. Jones* sub no. 1503 in Monte Loma, Sierra Leone, lect., in Herb. Mus. Brit. conservatus.

Green, making intricate patches closely applied to leaves or to the bark of shrubs. Strong shoots 0·8–1·0 mm broad, the stem 90 μm diam., with underleaves *c.* twice as wide as the stem. Leaves approximate or somewhat imbricate, complanate, spreading at an angle of 60–90° to the stem,

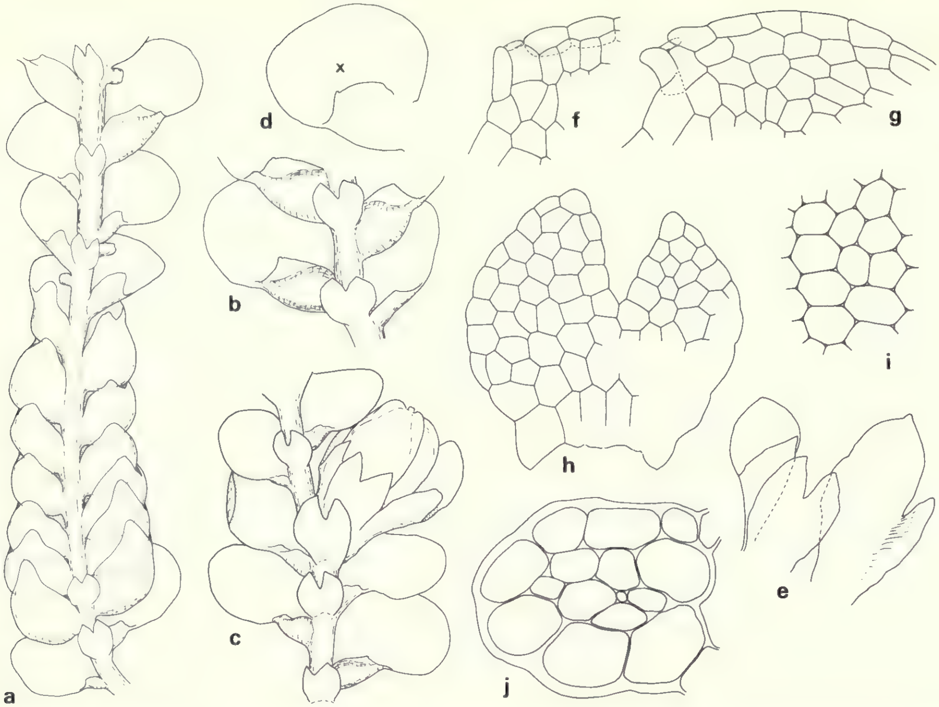

Fig. 7 *Lejeunea lomana* E. Jones. (a) male inflorescence; (b) part of shoot; (c) shoot with perianth. All ×40. (d) leaf, ×48; (e) female bracts and bracteole, ×48; (f) apex and (g) apex with free margin of lobule, compressed, ×240; (h) underleaf, ×240; (i) cells from 'x' on (d), ×240; (j) transverse section of stem, ×400. All drawn from *Jones* 1503 (holotype).

gently convex, ovate or oval, 0·46–0·53 × 0·34–0·45 mm, the base truncate, antical margin arched, apex broadly rounded, postical margin gently arched and making a wide shallow sinus with the gently arched keel. Well developed lobule about half the length of the lobe (measured from stem to apex), oblong-oval, inflated along the keel and proximally but the apical part flat and lying against the lobe, with most of the free margin readily visible *in situ*; the free margin of six cells (in addition to the cell in the notch proximal to the apical tooth); the apical tooth long, *c.* 13 × 40 μm, slightly curved, in line with the margin of the apex and free only at its rounded tip; hyaline papilla inserted on the side of the tip of the tooth and lying along the free margin.

Subapical cells of leaf 17–20 × 19–23 μm, averaging 18 × 21·6 μm, median cells 18–24 × 24–35 μm, averaging 22 × 26 μm, cells of antical margin 15–18 × 16–20 μm, and 3–4 rows in from the antical margin 15–22 × 20–24 μm, walls thin, trigones small or medium but distinct, intermediate thickenings absent, cuticle finely punctate; oil bodies 2–6 per cell, compound, subspherical, oval or fusiform.

Underleaves 1½–2 times as wide as the stem, orbicular, 150–180 μm wide and long, bilobed to the middle, the lobes broadly triangular, 5–6 cells broad at the base, with V-shaped sinus.

Stem in transverse section with seven cortical cells 15–20 μm wide, their outer walls 2–3 μm thick, their radial walls thin, over six medullary cells, 10–15 × 10–20 μm, thin-walled with slight thickening at wall junctions.

Dioecious. Male plants profusely branched, androecia large, of (2)–6–7 pairs of closely imbricate bracts with two basal underleaves only, intercalary on long shoots. Gynoecia on long shoots, with one innovation, the first leaf of which is a lateral leaf. Female bracts obovate, 0·5–0·6 × 0·24–0·33 μm, the apex broadly rounded, lobules about 2/3 as long, with keels 1/2–2/3 the length of the lobule, the keels straight or weakly inarched, that of the upper bract, and sometimes both keels, slightly winged with one row of projecting cells; the apices of the lobule of the upper bract, or of both lobules, acute. Bracteole oblong, about 2/3 the length of the bracts, bilobed to 1/3 its length. Perianth 0·5–0·8 × 0·33–0·5 mm, slightly exserted from the bracts, terete, pyriform, with five equal, rather low keels around the apex and upper half; the rostrum very variable, even in consecutive perianths, 20–80 μm long.

The preceding description relates to well-developed shoots; there are frequent abrupt transitions to lengths of shoot bearing smaller leaves with greatly reduced lobules, and such reduced leaves are normally present at the bases of branches and succeeding a male inflorescence.

SIERRA LEONE. Loma Mountains, 1520–1650 m (5000–5400 ft): gallery forest *c.* one km west of 'Camp 2', on leaves of *Memecylon, Morton* (*Harrington* 350 p.p., 351 p.p.), epiphyllous, *Jones* 1483 p.p., 1488 p.p., on small branches of shrubs, *Jones* 1479c, d & e, on dead branch, *Jones* 1495 p.p., 1497 p.p.; on margin of scrub in valley-head west of Bintimani, on bole of *Vernonia, Jones* 1503 (BM, holotype).

In all these collections, except *Jones* 1503, *Lejeunea lomana* was present in only small amounts, and mixed with other Lejeuneaceae. All collections were made in an area of about two km radius, but this circumscription is presumably due to the absence of any collecting beyond this area on the Loma plateau. Although the collections are small they are sufficient to show that within this area *L. lomana* is a well-defined taxon, and distinct from several other closely allied, and apparently as yet undescribed, species that occur elsewhere in the African mountains. One of these, which I collected in very small amount on Mont Cameroun (Cameroon Mountain) at 1220 m (4000 ft) in 1948 (*Jones* 310 p.p.), differs chiefly in being monoecious and having large underleaves two to three times as wide as the stem. Two other apparently different species were collected by Dr D. Steel in the Bale Mountains of Ethiopia, and I have other plants from East Africa awaiting study that may belong to the same complex. All have a lobule of closely similar structure, with a free margin of six to nine cells, and similar perianths and female involucres. They should probably be separated from the genus *Lejeunea,* but do not seem to fit well into any other existing genus. [E.W.J.]

11. **Lejeunea papilionacea** (Stephani) E. Jones in *J. Bryol.* **7**: 42 (1972).

Prionolejeunea aberrans Stephani, *Sp. hepat.* **6**: 387 (1923).

SIERRA LEONE. Masimo, epiphyllous, *Marmo* 160 p.p. Kambui Hills, Bambawo, epiphyllous on low vegetation near stream, *Harrington* 415 p.p., 417 p.p., 440 p.p.

GHANA. Ankasa River F.R., epiphyllous, abundant, *Jeník*; on palm leaves in swamp forest one mile south of the Ankasa bridge, *Jones* 1382 p.p.

A local species allied to *Lejeunea caespitosa,* usually though not exclusively epiphyllous, and known elsewhere only from Cameroon and (as *Prionolejeunea aberrans*) Madagascar. Schuster (1980) has recently transferred it to *Cardiolejeunea* R. M. Schuster & Kachroo.

12. **Lejeunea ramosissima** Stephani in *Bot. Jb.* **8**: 88 (1886 ['1887']); E. Jones in *Trans. Br. bryol. Soc.* **5**: 300 (1967).

Lejeunea eplicata Stephani, *Sp. hepat.* **5**: 711 (1915); E. Jones in *Trans. Br. bryol. Soc.* **5**: 303 (1967).

SIERRA LEONE. Loma Mountains, 1370–1830 m (4500–6000 ft): 'sur rameaux d'Eugenia, forêt relique d'altitude vers 1850 [sic]m', *Jaeger* 1188 p.p. (PC); on tree boles on margin of forest near 'Camp 2', *Harrington* 159 p.p. *Jones* 1472b, 1478; on tree boughs in gallery forest west of Bintimani, *Harrington* 327; epiphyllous in forest, *Harrington* 299, *Jones* 1483a p.p., 1488; in rock crevices, *Harrington* 227, 323 p.p.

A montane species which is abundant in the forest on Mont Cameroun (Cameroon Mountain) from *c.* 1320 m upwards, and also recorded from the Congo Republic (Pócs, 1980), São Tomé, Pagalu, and from the Nimba Mountains (*Schnell* 3525, PC) and the Macenta Massif (*Lisowski*, OP and Herb Jones) in Guinea. Grolle (1978) notes that it is frequent at altitudes of 320–790 m in the Seychelles. Its occurrence in the East African mountains is doubtful. A dioecious species in which perianths are often rare or absent, it cannot be separated vegetatively from *Lejeunea brenanii*. Male inflorescences of *L. ramosissima* have underleaves only at the base, whereas those of *L. brenanii* have underleaves throughout their length. *Jones* 1488 has perianths which are bluntly angled near the apex, and thus resembles *L. eplicata* Stephani, and helps to demonstrate the identity of the two taxa.

13. **Lejeunea setacea** Stephani in *Bull. Mus. natn. Hist. nat. Paris* **18**: 120 (1912); E. Jones in *Trans. Br. bryol. Soc.* **5**: 784 (1969).

SIERRA LEONE. Freetown Peninsula, Mount Aureol, earth bank of path, *Jones* s.n. Musaia Agricultural Station, pumping station, on tree bole, *Haswell* B1 p.p. Njala, in crown of *Nauclea diderrichii, Deighton* 5313 p.p. Bo, *Gardner* 128. Jawo near Kenema, by the Moa river, abundant on tree branches and boles at top of and just above the flood zone, *Jones* 1536.

GHANA. Krokosua Hills, on cocoa in farm between the Forest Reserve and Bia bridge, *Jones* 1388 p.p. Kwahu-Tafo (6°39′N, 0°40′W), on cocoa, *Jones* s.n. Brukru Rock near Kwahu-Tafo, on shaly sandstone, *Jones* 1417. Aburi Botanical Gardens, on root of *Hura, Jones* s.n. Kpedze Rest House, on cocoa, *Jones* s.n.

A lowland species, widely distributed throughout the wetter parts of the Guinea region of West Africa and the Congo Basin. The leaves are flat and the shoots strongly complanate – a feature that helps with recognition in the field. Outside this area it has been recorded only with doubt from south-eastern Kenya by Pócs (Bizot & Pócs, 1974), though it is closely allied to, and possibly conspecific with, the South American *Lejeunea pililoba* Spruce. Schuster (1980) has recently transferred both taxa to *Rectolejeunea*.

XXXI. **LEPTOLEJEUNEA** (Spruce) Schiffner

1. **Leptolejeunea astroidea** (Mitten) Stephani, *Sp. hepat.* **5**: 363 (1913); Vanden Berghen in *Bull. Jard. bot. État Brux.* **23**: 68 (1953).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., *Harrington* 85, 89a p.p., 90, 99 p.p. etc., *Jones* s.n.; Leicester Peak, *c.* 550 m (1800 ft), in forest near summit, *Jones* 1428; Sugar Loaf Gap, on low vegetation in forest, *Harrington* 652 p.p.; Bathurst, Kongo Dam, *Jones* s.n.; Guma Valley, in mature forest, *Harrington* 101 p.p., 102 p.p.; Black Johnson Beach near York, on low shrub in thicket behind the beach, *Harrington* 16; York Pass, forest understorey, *Harrington* 625 p.p., 630 p.p.; Picket Hill, forest near summit, *c.* 850 m (2800 ft), *Gledhill* s.n. Masimo, *Marmo* 160 p.p., 161 p.p. Bo, near the school, *Revell* (Herb. Jones). Kambui Hills, Bambawo, in forest on plateau, *c.* 370 m (1200 ft), *Harrington* 411 p.p., 412 p.p., 421 p.p., 483 p.p., 484 p.p., 485 p.p., *Jones* 1543b. Giema, in secondary forest, *Harrington* 512 p.p., 549 p.p. Gola Hills, near Lalehun, *Marshall* s.n.; by river, *Jones* s.n.

GHANA. Krokosua Hills F.R., 490–550 m (1600–1800 ft), abundant on low shrubs in small gaps, *Jones* 1396. Ankasa River F.R., leaves in crown of *Glutea, Jones* 1378c. Subri F.R., on *Raphia* fronds in swamp forest, *Jones* 1355 p.p.

A lowland species, rarely ascending above 800 m, though it has been recorded as high as 1000 m in the Macenta region of Guinea (Duda & Vanden Berghen, 1967); widely distributed throughout the 'rain forest' districts of West Africa and the Congo. It appears to need shelter and high atmospheric humidity, and is almost invariably epiphyllous on herbs and low understorey shrubs. It is exceptional for it to occur as an epiphyll in the crown of a large tree, as in *Jones* 1378c, which, it should be noticed, was close to a river in a district of very high rainfall. It is often associated with the other two species of *Leptolejeunea,* and is perhaps the most abundant of the three. Like many other epiphyllous hepatics it requires more light than reaches the floor of the unbroken dense forest, and tends to occur beneath slight gaps in the canopy or in thin-canopied forest.

2. **Leptolejeunea maculata** (Mitten) Schiffner, *Consp. hepat. archip. ind.*: 275 (1898); Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **47**: 213 (1977).

Leptolejeunea thomeensis (Stephani) Stephani, *Sp. hepat.* **5**: 366 (1913); Vanden Berghen in *Revue bryol. lichén.* **32**: 50 (1963).

Leptolejeunea truncatiloba Stephani, *Sp. hepat.* **5**: 368 (1913); Vanden Berghen in *Bull. Jard. bot. État Brux.* **23**: 65 (1953).

SIERRA LEONE. Gola Hills, near Lalehun, on low vegetation in forest, *Marshall* s.n.

GHANA. Krokosua Hills F.R., 490–550 m (1600–1800 ft), abundant with *Leptolejeunea astroidea, Jones* 1396 p.p. Ankasa River F.R., on leaves in crown of *Glutea, Jones* 1378c p.p. Aiyinasi A.R.S., on *Citrus* leaves, *Jones* 1385 p.p. Pra-Suhien F.R., widely distributed on herbs in regenerated forest, *Jones* 1345b & c.

Leptolejeunea maculata closely resembles *L. astroidea* in its general ecological requirements and, in W. Africa, the two species are usually associated. Unlike *L. astroidea* it occurs in the lowland rain forest of East Africa (e.g. at Amani in Tanzania), and extends to the Mascarenes.

3. **Leptolejeunea quintasii** Stephani, *Sp. hepat.* **5**: 365 (1913); Vanden Berghen in *Bull. Jard. bot. État Brux.* **23**: 70 (1953); *Revue bryol. lichén.* **32**: 51 (1963).

SIERRA LEONE. Giema, in secondary forest, *Harrington* 528 p.p., 548 p.p., 549a p.p. Gola Hills: near Lalehun, *Marshall* s.n., abundant by stream in forest, *Jones* 1553b; Gola North F.R., abundant in unexploited 'moist forest', *Jones* 1568 p.p.

GHANA. Subri F.R., on *Raphia* fronds in swamp forest, *Jones* 1355 p.p. Kade A.R.S., very abundant in swamp forest on herbs, and on the forest margin, *Jones* 1222. Opposite Kade, in swamp on the Kadeva rivulet, on *Raphia hookeri, Jeník* (Herb. Jones & OP).

Like *Leptolejeunea maculata, L. quintasii* extends eastwards through the Congo Basin to the lowland rain forest of East Africa, but has not been recorded from western Sierra Leone.

Two or more of the three species of *Leptolejeunea* often grow together. When the leaves on which they have been growing are dried without undue pressure, the three species can be seen to differ in the positions assumed by their own leaves when dry. The leaves of *L. quintasii* remain flat and appressed to the substratum; those of *L. astroidea* become channelled by the up-curving of antical and postical margins, and remain spreading or obliquely ascending, while those of *L. maculata* roll longitudinally and stand up vertically, perpendicular to the substratum. Harrington found that plants are intensely fragrant when fresh, and their presence on a leaf can readily be detected by the nose. Presumably the fragrance emanates from the oil bodies in the ocelli, which differ somewhat in appearance; those of *L. astroidea* are finely granular and very highly refractive, appearing almost homogeneous, whereas those of *L. maculata* are coarsely granular and opaque.

XXXII. **LOPHOCOLEA** (Dumort.) Dumort.

1. **Lophocolea concreta** Montagne in *Annls Sci. nat.* (Bot.) III, **4**: 350 (1845); Grolle in *Trans. Br. bryol. Soc.* **3**: 595 (1959).

Lophocolea subrotunda Mitten in *Phil. Trans. R. Soc.* **168**: 396 (1879); E. Jones in *Trans. Br. bryol. Soc.* **2**: 175 (1953).

SIERRA LEONE. Loma Mountains: in valley forest between Seradu and Kurubonla, 610 m (2000 ft), on rotten log, *Jones* 1519; in forest between 'Camp 1' and Sokurela, on rotten bough, *Harrington* 383; in forest above Sokurela, 1070 m (3500 ft), on rotten log, *Jones* 1511, and at 940 m (3100 ft), *Jones* 1512 p.p.

GHANA. Subri F.R., on rotten log, *Jones* ! Amedzofe, shaded rock near summit of hill, *Jones* 1255a (GC).

Widely distributed in tropical Africa; perhaps somewhat montane, and mostly in climates with a strong dry season. Thus it is likely that it is much more abundant in the drier parts of Sierra Leone and Ghana than the above records suggest.

2. **Lophocolea difformis** Nees, *Syn. hepat.*: 166 (1845); Grolle in *Trans. Br. bryol. Soc.* **3**: 596 (1959).

Lophocolea molleri Stephani in *Bot. Jb.* **8**: 83 (1886 ['1887']); E. Jones in *Trans. Br. bryol. Soc.* **2**: 181 (1953).

SIERRA LEONE. Loma Mountains, forest in centre of plateau, on fallen bough, *Morton* (*Harrington* 366, 370).

GHANA. Rocks in steep roadside bank between Vane and Amedzofe, *c.* 610 m (2000 ft), *Jones* 1264.

Widespread in tropical and warm temperate Africa, but, like *Lophocolea concreta*, chiefly in country with a moderate rainfall and strong dry season, and thus likely to be more abundant than the above records suggest.

3. Lophocolea martiana Nees, *Syn. hepat.*: 152 (1845), subsp. **newtonii** (Stephani) R. M. Schuster, *Hepat. Anthocerot. N. Amer.* **4**: 237 (1980).

Lophocolea congoana Stephani in *Bull. Soc. r. bot. Belg.* **41**: 119 (1904); Grolle in *Trans. Br. bryol. Soc.* **3**: 597 (1959).

Lophocolea newtonii Stephani, *Sp. hepat.* **3**: 170 (1907); E. Jones in *Trans. Br. bryol. Soc.* **2**: 188 (1953).

SIERRA LEONE. Kambui Hills, Bambawo, steep earth bank by path, *Harrington* 443, 445 p.p.; rotten logs in forest, *Jones* 1528, 1544, 1545. Gola North F.R., on rotten log, *Jones* 1566a.

GHANA. Bia North F.R., on rotting logs in forest, *Jones* ! Krokosua Hills F.R., 550 m (1800 ft), on grass tussock in open 'glade', *Jones* 1400. Tarkwa, *Saxby* (CGE). Ochi Headwaters F.R., *West-Skinn* 159. Esukawkaw F.R., *Jeník* (Herb. Jones). Begoro, *Jones* ! Southern Scarp F.R., *Jones* ! Atewa Hills F.R., on bole of large tree in swamp forest, *Jones* 1331 (GC). Amedzofe, on steep cliff near the waterfall, *Irvine* 411.

A common species throughout the lowland rain forest of West Africa and the Congo Basin, extending also into East Africa, where it is much more local. The lack of records from western Sierra Leone is noteworthy; presumably it is a species for which the dry season of the Freetown Peninsula is too severe, nor does it occur freely in young secondary forest. It is commonest on rotting logs, but is also frequent on the bases of tree boles, and is very often associated with *Chiloscyphus dubius*. On rotting wood *Arachniopsis diacantha* and *Cephalozia fissa* are common associates. It is less frequent on earth and rock.

XXXIII. **LOPHOLEJEUNEA** (Spruce) Schiffner

1. Lopholejeunea abortiva (Mitten) Stephani, *Sp. hepat.* **5**: 70 (1912); Vanden Berghen in *Revue bryol. lichén.* **39**: 376 (1973).

SIERRA LEONE. Freetown Peninsula: Dighton Dam No. 1, valley below Sugar Loaf, on boulder above the dam, *Harrington* 661 p.p.; York Pass, by stream, *Harrington* 628 p.p. Giema, on partly submerged boulder in stream, *Harrington* 538, 539.

GHANA. Southern Scarp F.R., near Bunso, on bole of small tree, *Jones* s.n. Amedzofe, on wet rocks in stream just above the waterfall, *Jones* 1278a.

Specific distinctions in the genus *Lopholejeunea* are frequently indistinct; *L. abortiva* is closely allied to the much more abundant *L. fragilis,* of which it may prove to be a hygromorphic state. It frequently grows, like *Jones* 1278a, in wet places close to streams, though it may also grow on tree boles and on fallen logs. Apart from being a somewhat larger plant than *L. fragilis* it is said to differ in the absence of a dorsal keel to the perianth, in the female bracteole being oboval (not suborbicular), and in the lobules of the female bracts being small (often more than half the length of the bract in *L. fragilis*), but there is much variation in all these features. A low dorsal keel may be present or absent, even in the same colony, but the keel is not winged, as it usually is in *L. fragilis.*

2. Lopholejeunea fragilis Stephani, *Sp. hepat.* **5**: 65 (1912); Vanden Berghen in *Bull. Jard. bot. État Brux.* **20**: 176 (1950).

SIERRA LEONE. Freetown Peninsula, Leicester Peak, on bole of old mango, 440 m (1450 ft), *Jones* 1464; on boulder in open forest near the summit, *Brenan* (*Jones* 466); on tree bole in low forest near the summit, *Brenan* (*Jones* 476 p.p.); on rocks, 520 m, *Jones* 1452b. Kabala, on mango near the District Officer's bungalow, *Harrington* 140 p.p. Lake Sonfon, epiphyte in forest surrounding the 'lake', *Harrington* 28 p.p. Loma Mountains: forest between Seradu and Kurubonla, 610 m (2000 ft), on tree boles, *Jones* 1515 p.p., 1520b, 1521 p.p., on *Uapaca, Jones* 1522b; Seradu, in forest by the village, 610 m (2000 ft), *Jones* 1517a; above Sokurela, 910–1220 m (3000–4000 ft), on tree boles in forest, *Jones* 1468a. Masimo, *Marmo* 160 p.p. Kambui Hills, Bambawo, on mango on edge of forest, *Harrington* 434, 437 p.p.; on trees near the Rest House, *Harrington* 569 p.p., *Jones* 1527 p.p.

GHANA. Ankasa River F.R., on twigs of *Samanea* by the river, *Jones* 1377a. Pra-Suhien F.R., side of tree root, *Jones* 1343c.

Widely distributed throughout West Africa and the Congo Basin, and extending more locally to Mozambique, Natal, and Transvaal; usually on bark, rarely on rock.

3. **Lopholejeunea jonesii** Vanden Berghen in *Bull. Jard. bot. État Brux.* **20**: 178 (1950).

SIERRA LEONE. Loma Mountains, frequent on tree boles in the forest from *c.* 1520 m (5000 ft) upwards: near 'Camp 2', on tree boles, *Jones* 1483b, on lianes, *Jones* 1476b, 1495b; between Dawule and Bintimani, *Harrington* 239 p.p.; forest west of Bintimani, *Harrington* 325 p.p., 326 p.p., *Jones* 1497, 1500.

Previously known only from *c.* 2100 m on Mont Cameroun (Cameroon Mountain). *Lopholejeunea jonesii* differs from *L. subfusca* in its acute leaves and the large lobules of its female bracts, which resemble those of *L. fragilis*.

4. **Lopholejeunea subfusca** (Nees) Schiffner in *Bot. Jb.* **23**: 593 (1897); Vanden Berghen in *Bull. Jard. bot. État Brux.* **20**: 173 (1950); *Revue bryol. lichén.* **39**: 381 (1973).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., on lianes in forest, *Harrington* 92, 596 p.p., bole of tree near Heddle's Farm, *Jones* s.n.; Havelock Plateau, on small tree in scrub, with *Schiffneriolejeunea polycarpa, Jones* s.n.; Regent, trees in farm bush, *Harrington* 408 p.p., 409 p.p.; three km north-east of Toke, on small tree in thicket, *Jones* 1448b. Kasewe F.R., on lateritic boulder in bed of forest stream, *Richards* R7171 (no perianths seen). Kambui Hills, Bambawo, on mango on edge of forest, *Harrington* 427 p.p., 437 p.p.; on small *Drypetes* in young-growth forest, *Jones* 1532a. Giema, on sapling, *Harrington* 554 p.p.

GHANA. Krokosua Hills F.R., on exposed stems of pioneer shrubs on forest margin, *Jones* 1401a. Ankasa River F.R., on trunk of *Parinari glabra, Richards* (GC 36676). Aiyinasi A.R.S., on small tree by Rest House, *Jones* 1363a; on 17–18 year-old *Citrus, Jones* 1383. In low secondary bush near Esiama, *Jones* 1365. Asanta, on coconut palms on the beach, *Jones* 1359 p.p. Bunso, on cocoa, *Jones* 1317b. Tafo Cocoa Research Inst., in garden, *Jones* 1333. Pra-Suhien F.R., bole of small tree, *Jones* 1337b p.p. Kade A.R.S., upper branches of *Parinari excelsa, Hossain* (GC 36700); upper branches of *Aningeria, Hossain* (GC 39324). Amedzofe, on *Combretum* in savanna woodland just below summit of the hill, *Jones* 1256 p.p. (GC).

A lowland species, widely distributed and often abundant in the moister districts throughout West Africa and the Congo Basin, and extending to the coastal districts of Kenya and Tanzania, and to Madagascar. It is also known from tropical America, Malaysia, Indonesia, etc., and is doubtless pantropical. It is probably photophilous, and commonly occurs on isolated trees, on the boles of trees in plantations, young farm bush, etc., and in the crowns of forest trees, rather than in the forest understorey. It is very variable, especially in the shape of the female bracteole, which may vary from obovate to almost semicircular, and the size and form of the perianth wings. The female bracts are obovate with small lobules, whereas in *Lopholejeunea fragilis* they are oval and more or less acute, with large lobules. The mature perianth is almost immersed in the bracts, whereas in *L. fragilis* the perianth emerges and is readily visible. The two species also differ in colour, *L. subfusca* typically being chestnut brown, while *L. fragilis* is blackish brown.

XXXIV. **MARCHANTIA** L.

1. **Marchantia planiloba** Stephani in *Bolm Soc. broteriana* **4**: 181 (1886); Vanden Berghen in *Revue bryol. lichén* **29**: 51 (1960).

GHANA. *Marchantia planiloba* is in cultivation at the Department of Botany, Reading University; the records indicate that the original stock was collected in Ghana by Professor T. M. Harris; the locality is unknown.

Marchantia planiloba and the closely allied *M. parviloba* Stephani (which Vanden Berghen *(op. cit.,* 1965) considers may be phenotypes of a single species) appear to be somewhat montane in their distribution; they might be expected to occur, for example, in the Atewa Hills. *M. parviloba* has been recorded chiefly from East Africa, but also from São Tomé and Mont

Cameroun (Cameroon Mountain), whereas *M. planiloba* has been recorded from São Tomé and Burundi.

2. Marchantia wilmsii Stephani in *Hedwigia* **31**: 126 (1892); Vanden Berghen in *Résult. scient. Explor. hydrobiol. Bassin Lac Bangweolo & Luapula* **8** (1): 178 (1972).

Marchantia chevalieri Stephani ex Bonner in *Candollea* **14**: 103 (1953).

SIERRA LEONE. Njala, abundant on the bank of the river on mudstones between highest and lowest river level, *Deighton* 2870; on clay at the river bank, inundated in the wet season, *Deighton* 6032. Loma Mountains, Sokurela, stream bank near the village, *Harrington* 142.

GHANA. Aiyinasi, banks of river Fiakpole, *Jones* 1360. Kibi ['Kibbi'], on damp shady bank in evergreen forest, *Irvine* 26. Road cutting between Kibi and Bunsu ['Bunso'], ten miles from Kibi, (perhaps the same locality as *Irvine* 26), *Boughey* (Herb. Jones), det. Vanden Berghen. Buem-Krache District, waterfall at Shiare (*c.* 8°20′N, 0°40′E), *Hall* 1534 (Herb. Jones).

The commonest species of *Marchantia* in tropical Africa, extending southwards to Transvaal and Natal, and from sea-level to 1250 m or more. In the field it is readily distinguished from *M. parviloba* and *M. planiloba* by the presence of a dark median line on the dorsal surface of the thallus.

XXXV. MARCHESINIA Gray

1. Marchesinia excavata (Mitten) Stephani, *Sp. hepat.* **5**: 145 (1912); E. Jones in *Trans. Br. bryol. Soc.* **6**: 78 (1970).

Archilejeunea apiculata Pearson in *Annls Cryptog. exot.* **4**: 61 (1931).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., on bole of tree near Heddle's Farm, *Jones* 1420; Leicester Peak, 520 m (1700 ft), on boughs of *Combretum* in scrub, *Jones* 1453a; forest above Bathurst, 430 m (1400 ft), on bole of large *Dialium, Jones* 1436; Sugar Loaf Mountain, 700 m (2300 ft), on bark, *Tindall* 57 p.p.; Sugar Loaf Mountain, north side, on tree, *T. S. Jones* 333 p.p., 340 p.p.; Toke, on large *Chrysobalanops* at back of beach, *Jones* 1466a, and also in valley three km to north-east, *Jones* s.n. Lake Sonfon, on trunk of *Erythrophleum* in forest by 'lake', *Harrington* 54, 55. Bumban (9°07′N, 11°54′W), 200 m (650 ft), *Thomas* 2006. Mesima near Kalu ['Messima near Kailu'] (7°12′N, 11°46′W), on tree in coastal savanna, *Richards* (Herb. Jones). Gola North F.R., on main bole of large *Mimusops, Jones* 1559a; on upper bole and covering main boughs in crown of large tree, *Jones* 1562.

GHANA. Krokosua Hills F.R., 550 m (1800 ft), on bole of tree on forest margin, *Jones* 1404. Afram Headwaters F.R., in relic of natural forest, *Jones* s.n. Ankasa River F.R., on bole of *Samanea* by the river, *Jones* 1376b. Tarkwa, *Saxby* (CGE, sub *Archilejeunea apiculata*). Pra-Suhien F.R., on upper part of bole of tree, *Jones* 1338. Atewa Hills F.R., near top of bole of large *Lophira, Jones* 1318; on large branch of *Cassipourea, Hossain* (GC 36666). Aiyaola F.R., on bole of middle-storey tree, *Jones* 1239a.

A West African species, extending from Guinea to Zaire, and locally very abundant, especially in Sierra Leone. It usually grows on large trees, and has a preference for the upper parts of boles and boughs in the crowns, or the boles of isolated but sheltered trees; in such situations it often forms extensive sheets. It is essentially a lowland species.

2. Marchesinia moelleriana Pearson in *Ark. Bot.* **19** (5): 10 (1925); E. Jones in *Trans. Br. bryol. Soc.* **6**: 80 (1970); *J. Bryol.* **10**: 394 (1979).

SIERRA LEONE. Loma Mountains: gallery forest in centre of plateau, on large branch, *Morton* (*Harrington* 374 p.p.); near 'Camp 2', 1520–1680 m (5000–5500 ft), on lianes in forest, *Jones* 1479, 1495 p.p.; valley-head west of Bintimani, 1680 m, on *Vernonia* on margin of forest, *Jones* 1497a.

Marchesinia moelleriana is a montane species which appears to replace *M. excavata* at altitudes above 1000 m. It is known elsewhere from East Africa, where it extends from Mount Elgon to Rhodesia (now Zimbabwe); it has not been recorded from Cameroon, though it is to be expected there.

XXXVI. MASTIGOLEJEUNEA (Spruce) Schiffner

1. Mastigolejeunea auriculata (Wilson) Schiffner in Engl. & Prantl, *Nat. Pflanzenfam.* **1** (3): 129 (1893); Gradst. & Inoue in *Bull. natn. Sci. Mus. Tokyo* B, **6**: 25 (1980).

Mastigolejeunea carinata (Mitten) Stephani, *Sp. hepat.* **4**: 759 (1912); Vanden Berghen in *Bull. Jard. bot. État Brux.* **19**: 378 (1949).

SIERRA LEONE. Musaia Agricultural Station, on *Uapaca togoensis, Sellar* B4. Kabala, on tree near the District Officer's bungalow, *Harrington* 131; on boulder, 135. Secondary forest five km south of Kabala, *Harrington* 119a, 125 p.p. Between Seradu and Kurubonla, in valley forest, *Harrington* 400, *Jones* 1520. Bo, on tree stump, *Gardner* 130 p.p.

GHANA. Bia North F.R. north of Pampramasi, in crown of *Mansonia, Jones* 1411 p.p. Asenanyo F.R., in crowns of *Triplochiton* et al., *Jones* 1412 (GC), 1413a. Oda, on cocoa, *Irvine* 8a. Esukawkaw F.R., *Jeník*. Kade, abundant, *Jones* 1227a (GC). Tafo, trees in garden, *Jones* 1333. Aiyaola F.R., in crown of *Triplochiton, Jones* 1227a. Aburi Botanical Gardens, *Irvine* s.n., *Jones* s.n. (GC). South of Kpandu (7°N, 0°18′E), in savanna woodland, on *Bauhinia, L. E. Newton* 596. Amedzofe, in savanna woodland just below summit of the hill, *Jones* 1259e (GC).

Mastigolejeunea auriculata is widely distributed and polymorphic in tropical America and Africa. In West tropical Africa it extends from rain forest into savanna country with less than 1000 mm average annual rainfall. It is widely distributed and abundant in southern Ghana, especially on the boles of isolated trees and on branches in the crowns. In Sierra Leone it seems to be much more local, occurring chiefly in the drier districts in the north-east; the lack of records from the Freetown Peninsula and the Kenema district is remarkable.

2. Mastigolejeunea florea (Mitten) Paris in *Revue bryol.* **33**: 42 (1906); Vanden Berghen in *Bull. Jard. bot. État Brux.* **19**: 373 (1949).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., on tree bole, *Harrington* 581 p.p.; Havelock Plateau, on tree bole in scrub, *Jones* s.n.; Leicester Peak, on boulder in rather deep shade, *Brenan* (*Jones* 477); Regent, on small tree in farm bush, *Harrington* 408 p.p. Near road-bridge *c.* 32 km south-west of Kabala, on boulder, *Harrington* 404. Lake Sonfon, in forest surrounding the 'lake', *Harrington* 31, 47. Between Seradu and Kurubonla, in valley forest, 610 m (2000 ft), *Jones* 1520c. Loma Mountains, on large branch of tree in valley forest in centre of plateau, *c.* 1520 m (5000 ft), *Morton* (*Harrington* 374 p.p.). Kambui Hills, Bambawo, base of large tree, *Jones* 1551.

GHANA. Pampramasi, on tree root in stream bank, *Jones* 1410. Krokosua Hills: on boles of cocoa on western slopes, *c.* 300 m (1000 ft), *Jones* 1388 p.p.; on liane in forest, 490 m (1600 ft), *Jones* 1392a (GC); on trees on the margin of a 'glade', 550 m (1800 ft), *Jones* 1403b. Begoro, Southern Scarp F.R., *Jones* ! Tafo, on cocoa, *Thorold* TG.122 (BM & Herb. Jones); in garden, *Jones* ! Kade, *Hossain* (GC 39327). Aburi Botanical Gardens, *Foote* s.n., *Irvine* 23, *Jones* 1214a. Also *Cummins* s.n., without locality.

Widely distributed in West tropical Africa, but more local than *Mastigolejeunea auriculata*, and much less tolerant of dry conditions and exposed situations; it prefers some shade and often grows near water.

3. Mastigolejeunea nigra Stephani in *Bot. Jb.* **20**: 319 (1895).

Brachiolejeunea nigra (Stephani) Stephani, *Sp. hepat.* **5**: 115 (1912); Vanden Berghen in *Bull. Jard. bot. État Brux.* **21**: 90 (1951).

SIERRA LEONE. Musaia Agricultural Station, pumping station, epiphyte, *Haswell* Bl p.p. Loma Mountains, frequent between Sokurela and the upper margin of the forest from *c.* 910–1220 m (3000–4000 ft), on boles of large trees and on rocks, *Harrington* 382, on boulders, *Jones* 1470, on tree boles on the forest margin, *Jones* 1505. Kambui Hills, Bambawo, on mango on edge of forest, *Harrington* 437 p.p. Giema, on fallen tree in secondary forest, *Harrington* 536 p.p. Gola North F.R., boughs in crown of large tree, *Jones* 1572a.

GHANA. Amokwan Suezo, two miles south of the Ankåsa River bridge, on the roots of an epiphytic orchid which was collected for GC (Herb. Jones).

As widely distributed in tropical Africa as *Mastigolejeunea auriculata,* but more local. Although it may occur nearly at sea-level it tends to be montane, being more abundant at higher altitudes than *M. auriculata,* as can be seen in the Loma Mountains. It is also more restricted to exposed, well-illuminated habitats. In lowland rain forest it often seems to grow chiefly in the crowns of trees; the absence of records from this habitat in the Bia North, Aiyaola, Asenanyo, and Atewa Hills forest reserves in Ghana in remarkable. The absence of records from the Freetown Peninsula is also worthy of note.

4. **Mastigolejeunea turgida** Stephani, *Sp. hepat.* **4**: 762 (1912); Vanden Berghen in *Bull. Jard. bot. État Brux.* **19**: 376 (1949).

GHANA. Nsuta, by the Pra river, in the crown of a small *Scottellia, Jones* s.n.

A species which seems to be almost restricted to the crowns of trees, and therefore rarely gathered, but which is quite local. It was known hitherto only from a few collections in southern Nigeria, Cameroon, Bioko, and Príncipe.

XXXVII. **METZGERIA** Raddi

1. **Metzgeria saxbyi** Pearson in *Annls Cryptog. exot.* **4**: 70 (1931); Vanden Berghen in *Bull. Jard. bot. État Brux.* **19**: 200 (1948).

GHANA. Tarkwa, *Saxby.* Atewa Hills F.R., branch in crown of *Cassipourea, Richards & Hossain* (GC 36663); on lianes brought down by a fallen *Cassipourea, Jones* 1326 (confirmed by Y. Kuwahara); on small stems of shrubs close to ground in deep shade, in swamp forest, *Jones* 1329.

Evidently a locally abundant species in Ghana, *Metzgeria saxbyi* is one of the few monoecious members of the genus. It has also been recorded from Cameroon (Vanden Berghen, *op. cit.*). It is closely allied to the monoecious *M. conjugata* Lindb., from which it differs in having shorter marginal hairs which are mostly solitary, smaller cells in the wings of the thallus (40–45 μm wide × 55–65 μm long in *M. conjugata,* 25–35(–40) μm wide × 40–50 μm long in *M. saxbyi*), and more numerous hairs on the ventral surface of the wings; ventral hairs are, however, not present everywhere. *M. saxbyi* sometimes forms gemmae on the margins of the fronds.

It has not been possible to trace a type at MANCH, nor is *Metzgeria saxbyi* represented at CGE.

2. **Metzgeria thomeensis** Stephani in *Hedwigia* **30**: 271 (1891); Vanden Berghen in *Revue bryol. lichén.* **29**: 53 (1960); Kuwahara in *J. Hattori bot. Lab.* **40**: 287 (1976).

Metzgeria camerunensis Stephani, *Sp. hepat.* **1**: 293 (1899); Vanden Berghen in *Bull. Jard. bot. État Brux.* **19**: 192 (1948).

SIERRA LEONE. Freetown Peninsula: Leicester Peak, base of pole in dense scrub, *c.* 550 m (1800 ft), *Jones* 1427; Sugar Loaf Gap, intermingled with pendent mosses, *Harrington* 662 p.p. Loma Mountains: near 'Camp 1' in forest above Sokurela, 1220 m (4000 ft), on small bough, *Harrington* 253 p.p., same locality, on boulder, *Jones* 1473a, on bole of large tree, *Jones* 1509; forest near 'Camp 2', 1520–1680 m (5000–5500 ft), on tree trunk, *Harrington* 156, abundant on undershrubs, *Jones* 1484a.

GHANA. ? Subri F.R., on stems of shrublets in *Raphia* swamp, *Jones* s.n. ? Amedzofe, wet sheltered but well-lit rocks by stream just above the waterfall, *Jones* s.n.

Metzgeria thomeensis is widely distributed in West and East Africa. According to Kuwahara (*op. cit.*) it also occurs in Central and South America, Java, Sabah, and Papua New Guinea, and is thus pantropical.

3. **Metzgeria** sp.

SIERRA LEONE. Loma Mountains, 1370–1680 m (4500–5500 ft): *Jones* 1473b; in forest near 'Camp 2', *Harrington* 156, *Jones* 1479b; ibid., draping twigs of undershrubs, *Jones* 1484b; on *Vernonia* in scrub in valley-head north-west of Bintimani, *Jones* 1503c; on small tree, valley forest *c.* one km west of 'Camp 2', *Harrington* 331; valley forest in centre of plateau, *Morton* (*Harrington* 371).

The above collections represent a dioecious propaguliferous *Metzgeria* which becomes blue on drying, and is often mixed with *M. thomeensis*. Gemmiferous fronds are not markedly attenuate, and the gemmae, which are ecostate, are borne on the margins of the frond. Ventral hairs are lacking, except on the costa, and marginal hairs mostly solitary, 60–100 μm long. The costa varies considerably; most sections show two dorsal and four ventral cells, but in at least some of the specimens there are short lengths of costa with three or four dorsal cells, the number varying over a short distance, while the best developed of the collections (*Morton* (*Harrington* 371)) consistently has four dorsal cells. Medullary cells in transverse section of costa 14–16. Cells of wing 32–41 × 43–49 μm, often with minute trigones; cuticle in *Morton* (*Harrington* 371) and *Jones* 1503c finely and distantly papillose, in *Jones* 1473b, 1479b and 1484b smooth. Male involucres naked, female involucres with hairs 150 μm long. The plants seem to differ in one detail or another from all the species that have been described from Africa, but the specimens are inadequate for a satisfactory determination, nor is it certain that they all belong to the same taxon, though they probably do so.

Species of *Metzgeria* are far more widely distributed in the forest regions of both Sierra Leone and Ghana than the above records would imply, and additional species are probably present. The plants often grow as isolated fronds thinly scattered amongst other bryophytes, and they are most often sterile and possibly depauperate; well developed specimens with both sexes adequately represented can rarely be gathered. The fact that two or more species are sometimes mixed adds to the difficulty of determination.

The African species have been studied mainly by Vanden Berghen (1948, 1960*b*). More recently Kuwahara (1978) has studied the genus extensively, but he has examined few recent collections from Africa. His taxonomic treatment frequently conflicts with Vanden Berghen's, and clearly a much closer study of the variation within populations, based on careful field work, is needed before a satisfactory delimitation of the African species can be achieved.

XXXVIII. **MICROLEJEUNEA** Stephani

1. **Microlejeunea africana** Stephani in *Hedwigia* **27**: 61 (1888); E. Jones in *Trans. Br. bryol. Soc.* **5**: 777 (1969).

Lejeunea ulicina subsp. *africana* (Stephani) Vanden Berghen in *Résult. scient. Explor. hydrobiol. Bassin Lac Bangweolo & Luapula* **8** (1): 130 (1972).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., on trunk of *Dacryodes klaineana, Harrington* 586 p.p.; on the road to Hill Station, *Høeg* s.n.; Leicester Peak, *Jones* 1464 p.p.; Lumley Cove, *Jones* 468; York Pass, epiphyllous, *Harrington* 626 p.p. Musaia town, on mango, *Donald* s.n. Lake Sonfon, on edge of forest surrounding the 'lake', on mango, *Harrington* 24 p.p. Loma Mountains: Seradu, 610 m (2000 ft), in forest by the village, *Jones* 1515 p.p., 1517 p.p.; gallery forest *c.* one km west of 'Camp 2', 1520 m (5000 ft), on leaves of *Memecylon, Morton* (*Harrington* 348 p.p., 350 p.p., 351 p.p.). Njala, in crown of *Nauclea diderrichii, Deighton* 5313 p.p. Bo, near the school, epiphyllous, *Revell* (Herb. Jones). Kambui Hills, Bambawo, on low vegetation near pool in forest, *Harrington* 557 p.p. Giema, epiphyllous, *Harrington* 552b p.p. Gola Hills, Lalehun, low vegetation in forest, *Marshall* s.n.

GHANA. Krokosua Hills F.R., 490–550 m (1600–1800 ft), on leaves of low shrubs in forest, *Jones* 1396 p.p. Asanta, on coconut palms on the beach, *Jones* 1359 p.p. Aburi Botanical Gardens, *Jones* s.n. (GC). Amedzofe, on tree trunks amongst *Cheilolejeunea serpentina, Irvine* 412 p.p.

A widely distributed and common species, which is certainly far more abundant than the above records indicate; the inexperienced collector gathers it only by accident and the experienced collector avoids gathering it because it is too common. It usually grows on branches and twigs in the crowns of trees or shrubs, or on the boles of more or less isolated trees – not in the dense shade of the forest. It is less frequent though by no means rare as an epiphyll. It is closely allied to *Microlejeunea ulicina* (Taylor) A. W. Evans but as Jones (*op. cit.*) has shown there are sufficient differences to justify keeping the two taxa distinct. It is perhaps not a matter of great importance whether *M. africana* is regarded as a distinct species or merely as a subspecies, but the former procedure is more convenient in that it simplifies nomenclature.

There has been an increasing tendency in recent years to reunite the genus *Microlejeunea* with *Lejeunea*; this arises, perhaps, from stressing superficial features, rather than structural features, in the definition of the genera. If defined in terms of the characters enumerated by Jones (*op. cit.*)*, *Microlejeunea* forms a taxon which is better defined than some of the Lejeuneacean taxa which are generally accepted as genera.

2. **Microlejeunea ankasica** E. Jones in *J. Bryol.* **10**: 394 (1979).

? SIERRA LEONE. Freetown Peninsula, flaky bark of *Vitex* on bank of Mountain Torrent, *Jones* 1443d.

GHANA. Ankasa River F.R., on twigs in the crown of a *Vitex* by the river, *Jones* 1368 (BM, holotype). ?Kade, forest near the Agricultural Research Station, on smooth well-lit bole of *Maesobotrya,* chiefly around inflorescence-cushions, *Jones* 1218.

Microlejeunea ankasica closely resembles *M. kamerunensis*, but was described as differing in being autoecious, and in being completely devoid of innovations beneath the gynoecial bracts. *Jones* 1443d and *Jones* 1218 have innovations beneath the gynoecial bracts, but in other respects they agree completely with *M. ankasica.* This provides additional evidence for thinking that in the schizostipulean Lejeuneaceae the subgynoecial innovations do not have the taxonomic significance that they have in the holostipean Lejeuneaceae, where they are usually considered as providing generic characters (cf. *Lejeunea eckloniana*).

3. **Microlejeunea kamerunensis** Stephani, *Sp. hepat.* **5**: 812 (1915); E. Jones in *Trans. Br. bryol. Soc.* **5**: 782 (1969).

Lejeunea kamerunensis (Stephani) Vanden Berghen in *Bull. Jard. bot. natn. Belg.* **42**: 446 (December 1972), non *L. camerunensis* (Stephani) E. Jones (August 1972) (Art. 64.1).

SIERRA LEONE. Loma Mountains: *c.* 1680 m (5500 ft), on twigs of shrubs near 'Camp 2', *Jones* 1495 p.p.; epiphyllous in forest near 'Camp 2', *Jones* 1483a p.p.

Previously known from Cameroon and the East African mountains; most records are from moderately high altitudes, but some of those from Cameroon are from sufficiently low down to make it likely that the species will occur in Ghana.

XXXIX. **NOTOTHYLAS** Sulliv.

1. **Notothylas decurva** (Mitten) Stephani, *Sp. hepat.* **5**: 1020 (1917); Hässel de Menendez in *J. Hattori bot. Lab.* **41**: 23 (1976).

Notothylas angolensis Stephani, *Sp. hepat.* **5**: 1020 (1917).

SIERRA LEONE. Musaia, bare ground at base of *Ceiba pentandra, Sellar* B53.

GHANA. Mpraeso Scarp, in ditch near road, *Hall* 2631. Legon University Botanical Gardens, *Hall* (GC 47099 p.p.).

Apparently the commonest species of *Notothylas* in West Africa, and doubtless more frequent than the above records suggest.

2. **Notothylas indica** Kashyap in *Proc. Lahore philos. Soc.* **4**: 54 (1925).

GHANA. Legon University Botanical Gardens, mixed with *Notothylas decurva, Hall* (GC 47099 p.p.).

Notothylas indica differs from *N. decurva* in having black (not yellow) spores, a somewhat longer sporangium with a well developed persistent columella, and long narrow exothecial cells. The plant from Legon matches specimens from Lucknow, kindly provided by Professor Ram Udar. A plant from Sierra Leone (one mile south of Musaia town, on road bank under trees, *Donald* s.n.) agrees with *N. indica* in the sporangium wall, but has yellow spores.

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* Usually dioecious, the keels of the female bracts usually more or less winged, stem in transverse section with only three medullary cells, lobule inflated with round mouth and long curved apical tooth, cells of lobe small.

XL. **ODONTOLEJEUNEA** (Spruce) Schiffner

1. **Odontolejeunea tortuosa** (Lehm. & Lindenb.) Stephani, *Sp. hepat.* **5**: 173 (1912); Vanden Berghen in *Revue bryol. lichén.* **32**: 52 (1963).

SIERRA LEONE. Loma Mountains: forest near 'Camp 1', 1220 m (4000 ft), *Harrington* 293; gallery forest *c.* one km west of 'Camp 2', on leaves of *Memecylon, Morton* (*Harrington* 359, 362, 365 *et al.*); *c.* 1650 m (5400 ft), epiphyllous in forest by stream west of Bintimani (perhaps the same locality as *Morton*'s) *Jones* 1488a.

Locally abundant on the leaves of shrubs in the forest of the Loma plateau. A montane species with a wide, but disjunct, distribution in tropical Africa, usually at altitudes of 1500–1700 m, though a few records are from much lower altitudes, and the first African collection, by Palisot de Beauvois from 'Oware' (Warri), Nigeria must have been from near sea-level. It is thus possible that it occurs in Ghana, e.g. in the Ankasa River area or the Atewa Hills. Where it is found it usually seems to be abundant.

XLI. **PHAEOCEROS** Proskauer

1. **Phaeoceros laevis** (L.) Proskauer in *Bull. Torrey bot. Club* **78**: 347 (1951), subsp. **carolinianus** (Michaux) Proskauer, *Rapps Communs VIII Congr. int. Bot. Paris,* Sect. 14–16: 69 (1954); S. Arnell, *Hepat. S. Afr.*: 400 (1963).

SIERRA LEONE. Roadside one mile south of Musaia town, on rock under trees, *Donald* s.n.

Widely distributed in tropical and South Africa, and doubtless more frequent than the single record suggests. It is likely to occur in wet sites in drier parts of Sierra Leone and Ghana, where hepatics have not been collected.

XLII. **PLAGIOCHASMA** Lehm. & Lindenb.

1. **Plagiochasma eximium** (Schiffner) Stephani, *Sp. hepat.* **1**: 78 (1898); Bischler in *Revue bryol. lichén.* **44**: 248 (1978).

SIERRA LEONE. Loma Mountains, Bintimani, frequent on earth in crevices in the dolerite cliffs below the summit, 1830 m (6000 ft) upwards: *R. R. Glanville* 479, *Harrington* 181, 183, *Jones* 1485, det. H. Bischler.

Plagiochasma eximium is a montane species with a very wide but disjunct distribution; known also from Guinea, Cameroon, Zaire (Shaba), East Africa, Natal, southern Arabia, etc.

XLIII. **PLAGIOCHILA** (Dumort.) Dumort.

1. **Plagiochila africana** Stephani, *Sp. hepat.* **2**: 263 (1902); E. Jones in *Trans. Br. bryol. Soc.* **4**: 293 (1962).

SIERRA LEONE. Kambui Hills, Bambawo, in forest on twig of small tree, *Harrington* 414; epiphyllous, *Harrington* 441a.

GHANA. Ankasa River F.R., on branchlet of small tree by the river, *Jones* s.n.; epiphyllous on small shrub, *Jones* 1375 p.p. Pra-Suhien F.R., *Jones* 1337.

A lowland species, apparently restricted to the wetter parts of the West African forest from Cameroon, where it is frequent, westwards. Usually on small branches, lianes etc.; only exceptionally epiphyllous.

2. **Plagiochila barteri** Mitten in *J. Linn. Soc.* (Bot.) **22**: 320 (1886); E. Jones in *Trans. Br. bryol. Soc.* **4**: 276 (1962).

SIERRA LEONE. Presumably from the Freetown Peninsula, where, however, it has not been collected recently, *Barter* (NY, type). Loma Mountains: near 'Camp 1', 1220 m (4000 ft), on tree on margin of forest, *Harrington* 245; near 'Camp 2', 1520 m (5000 ft), on partly sheltered rock face in plateau grassland, *Harrington* 152.

A montane species, abundant in some of the East African mountains – e.g. on Kilimanjaro between *c.* 1850 and 2800 m – and also present, though apparently not abundant, on Mont Cameroun (Cameroon Mountain) and the islands of the Gulf of Guinea. On Príncipe it has been gathered from as low as 460 m, so Barter may have found it in 1857 in the hills close to Freetown at similar altitudes, where the forest is now secondary.

Plagiochila barteri seems to be uncommon on the Loma plateau.

3. **Plagiochila fusifera** Taylor in *J. Bot., Lond.* **5**: 268 (1846); E. Jones in *Trans. Br. bryol. Soc.* **4**: 311 (1962). Fig. 8.

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., side of partly buried boulder by bridge, *Harrington* 589; Guma Valley, on trees by road, *Harrington* 111. Lake Sonfon, on rotten bough in forest fringing stream, *Harrington* 36 (a depauperate form). Loma Mountains: near 'Camp 2', *c.* 1520 m (5000 ft), on trees in forest, *Harrington* 155, 157, 159, 297, 298, 318; sheltered rock in grassland, *c.* 1520 m, *Harrington* 152, *Jones* 1481; on *Vernonia* in scrub north-west of Bintimani, 1680 m (5500 ft), *Jones* 1497d p.p.; Bintimani summit plateau, *c.* 1940 m (6360 ft), in very sheltered crevices between boulders, *Harrington* 200 (leaves large enough for *Plagiochila divergens* but habit of *P. fusifera*); *c.* 1370 m (4500 ft), on sheltered boulder face in broken woodland, *Harrington* 231; branch in crown of tree on edge of forest, 1370 m, *Jones* 1504. Jawo near Kenema, branch of tree on bank of the river Moa, at the top of the flood zone, *Jones* 1540 (determination doubtful).

GHANA. Pra-Suhien F.R., bole of small tree in moderate shade, *Jones* 1336a. Atewa Hills F.R., on *Vernonia, Jones* 1325a. Amedzofe, on trees in old coffee farm, *Jones* 1246. Rocks in roadside bank above Vane, *Jones* 1267.

The plants grouped under the polymorphic *Plagiochila fusifera* form a taxonomically difficult complex. Jones (1962) tentatively distinguished three taxa in the group, *Plagiochila divergens* Stephani var. *divergens, P. divergens* var. *myriocarpa* (Pearson) E. Jones, and *P. fusifera,* but found it difficult to define clear boundaries between them; moreover poorly developed or atypical forms of *P. fusifera* might be difficult to separate from forms of *P. moenkemeyeri, P. praemorsa,* and *P. strictifolia.* The examination of many more specimens, especially from Tanzania and from West Africa, has neither reduced the difficulties nor suggested any better treatment.

Typical *Plagiochila divergens* var. *divergens* differs from typical *P. fusifera* in habit, size, and dentition of leaf: *P. divergens* is richly and regularly pinnately or bipinnately branched, forming large oblong or triangular fronds, the shoots 5–6 mm broad, with leaves 2·0–3·0 × 1·4–2·0 mm, the teeth long and sharp, ending in 1–3 uniseriate long cells, the apical cell about 30 μm long, twice as long as broad. *P. fusifera* is short, little branched, with an unbranched basal segment 10–14 mm long and 2·0–4·0 mm broad, and a head of a few subpinnate branches; leaves 1·4–1·7–(2·0) × 0·95–1·4 mm, the teeth short, broadly triangular, ending in 1–2 cells, the apical cell less than twice as long as broad, usually about as long as broad. *P. divergens* var. *myriocarpa* is intermediate in size (leaves 1·9–2·0 × 1·25–1·4 mm), but with the habit and dentition of *P. divergens.*

Some of the plants from the Loma Mountains (especially *Harrington* 157, 297, *Jones* 1504) have leaves which are in the size-range of var. *myriocarpa* and also resemble it in dentition, with the apical cells of the teeth up to 30 μm × 12–15 μm, but they resemble *Plagiochila fusifera* in habit, and they seem inseparable from more typical *P. fusifera* growing near by. Yet other plants from Loma, notably *Harrington* 200, have leaves which are large enough for var. *divergens,* though with short teeth and *P. fusifera* habit. The plants show very great variation in the degree to which the postical leaf-bases are ampliate, thus forming a ventral crest, and also in the development of trigones.

Jones (*op. cit.*) commented that '*P. fusifera* appears to be characteristic of the country with a sufficiently high rainfall but a strong dry season'; the records for Sierra Leone and Ghana agree with this statement. Thus in Ghana the species seems to be uncommon in the forest districts, and was not found in the wet west.

4. **Plagiochila integerrima** Stephani in *Bolm Soc. broteriana* **4**: 173 (1886); E. Jones in *Trans. Br. bryol. Soc.* **4**: 267 (1962).

SIERRA LEONE. Loma Mountains: near 'Camp 1', 1220 m (4000 ft), on boulder by stream in forest, *Harrington* 270a, b; near 'Camp 2', 1520 m (5000 ft), on stone in stream in forest, *Harrington* 162. Kambui Hills, Bambawo, in forest on small tree root, partly submerged in stream, *Harrington* 465. Giema, on boulders in and by stream (periodically submerged) in secondary forest, *Harrington* 520.

GHANA. Pampramasi, by stream in forest, *Jones*! Ochi Headwaters F.R., *West-Skinn* 181, 186. Assin Cocoa Station (?5°42′N, 1°17′W), *West-Skinn* 129. Asuansi (5°18′N, 1°14′W), at side of river Kakum, *H. E. Box* 2080. Agogo, *Foote* 16. Begoro, on rocks below the waterfall, *Jones* ! Southern Scarp F.R., by stream, *Jones* ! Atewa Hills F.R., on tree boles in swamp forest (the 'Kaolin Swamp'), *Jones* 1331 (GC); on stones in stream, *Jones* ! Bunso, *Foote* s.n.

Perhaps the most generally distributed *Plagiochila* of tropical Africa, frequent throughout a wide range of rainfall regimes and altitudes, but always in wet places around springs, streams etc., often in deep shade. The absence of records from the Freetown Peninsula is remarkable. *P. integerrima* probably needs sites that are permanently moist, and the Freetown streams may be too seasonal in their flow and too torrential in the rains.

5. **Plagiochila moenkemeyeri** Stephani, *Sp. hepat.* **2**: 412 (1904); E. Jones in *Trans. Br. bryol. Soc.* **4**: 321 (1962). Fig. 8.

SIERRA LEONE. Freetown Peninsula: Leicester Peak, abundant from *c.* 520 m (1700 ft) upwards, on boles of small trees and on twigs of shrubs, both in deep shade and in open rocky ground, *Brenan* (*Jones* 476), *Jones* 1430, 1431, 1459, 1460, 1461b, 1462a, and less frequently on rocks, *Brenan* (*Jones* 477), *Jones* 1458a; Regent, *Irvine* 218; Sugar Loaf Gap, on understorey shrubs and small trees, *Harrington* 648; York Pass, on small tree, *Harrington* 611a. Loma Mountains: forest between Sokurela and 'Camp 1', 910–1220 m (3000–4000 ft), *Jones* ?1471b; forest in valley near 'Camp 2', *c.* 1650 m (5400 ft), intimately mixed with *Plagiochila fusifera, Jones* ?1481a; near 'Camp 1', on small tree in forest, 1220 m (4000 ft), *Harrington* 255, 263.

GHANA. Krokosua Hills F.R., 520–550 m (1700–1800 ft), on stems of small shrubs in forest, mixed with *Plagiochila strictifolia, Jones* 1397b. Aburi Botanical Gardens, *Jones* s.n. Amedzofe, on trees in cocoa farms above the waterfall, frequent, *Jones* 1271a.

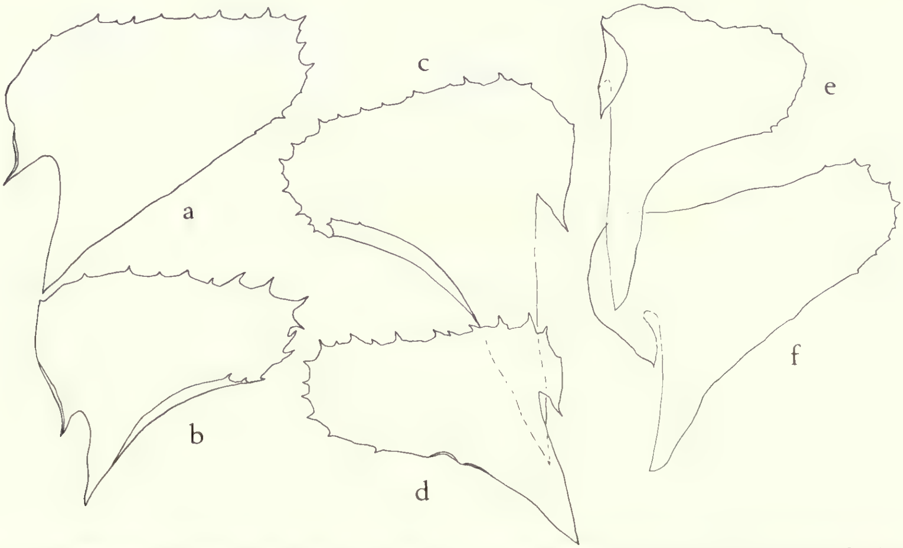

Fig. 8 (a), (b) leaves of *Plagiochila fusifera* Taylor. (a) *Harrington* 589 from Fourah Bay College B.R.; (b) *Harrington* 297 from the Loma Mountains – like some other specimens from here more coarsely and irregularly dentate than in the usual lowland forms of *P. fusifera.* (c)–(f) leaves of *Plagiochila moenkemeyeri* Stephani. (c) *Jones* 1430 from Leicester Peak, base of tree in small gap, open situation in rocky ground; (d) *Jones* 1462a from Leicester Peak, vertical bole of tree in deep shade; (e) *Jones* 1271a from Amedzofe; (f) *Jones* 1471b from the Loma Mountains – form with postical bases of leaves making a well-marked crest and antical bases more shortly decurrent than in typical *P. moenkemeyeri,* though more longly decurrent than in *P. fusifera.* All ×20.

Plagiochila moenkemeyeri is predominantly, if not exclusively, a West African species which is abundant in the region of the Bight of Biafra and is widely distributed through the forest region to the west, though perhaps local. It tends to be montane, although there are records from near sea-level in Nigeria. It is very variable, and forms occur which are difficult to separate from *P. fusifera,* though typically the two species are quite distinct. *P. moenkemeyeri* is more rigid, with more open, apparently dichotomous branching, and the dorsal leaf bases are more longly decurrent and much longer relative to the ventral base (Fig. 8). The trigones tend to be larger than in *P. fusifera,* and often somewhat nodular, though they are sometimes small. The longly decurrent dorsal leaf bases and the tendency of the ventral bases to form a crest may also give rise to difficulty in distinguishing *P. moenkemeyeri* from depauperate forms of *P. pinniflora*, though well developed forms of the two species are very different.

The queried numbers from the Loma Mountains are determined with doubt. *Jones* 1471b and 1481a have leaves which are more shortly decurrent dorsally than in typical *Plagiochila moenkemeyeri,* with a tendency for the dorsal wing to be abruptly contracted at its base, and the trigones are quite small; the ventral bases are more strongly ampliate than in typical *P. moenkemeyeri,* and form a strong ventral crest. These plants may possibly represent a different taxon.

6. **Plagiochila neckeroidea** Mitten in *Trans. Linn. Soc. Lond.* **23**: 57 (1860); E. Jones in *Trans. Br. bryol. Soc.* **4**: 291 (1962).

SIERRA LEONE. Freetown Peninsula, Fourah Bay College B.R., on bole of tree in valley, *Jones* s.n. Gola North F.R., fallen from tree in unexploited forest, *Jones* 1570b.

GHANA. Krokosua Hills F.R., 550 m (1800 ft), on bole of tree on margin of forest, *Jones* 1404. Pampramasi, on bole of pole-tree in small gap in forest, *Jones* 1408. Ankasa River F.R., abundant on stems of small shrubs near the river, *Jones* 1375; occasionally epiphyllous, *Jones* 1375 p.p., *Jeník* (Herb. Jones & OP). Subri F.R., *Jones* ! Pra-Suhien F.R., on boles of small trees, *Jones* 1337a. Ochi Headwaters F.R., *West-Skinn* 144, 189. Kade A.R.S., bole of small tree in swamp forest, *Jones* 1224b.

Plagiochila neckeroidea is frequent throughout the lowland rain forest of West Africa, and extends into the Congo Basin. It seems to require high atmospheric humidity, and is thus frequent in swamp forest, by rivers, and around very sheltered gaps in the forest, though never where liable to be submerged. It is a very distinct species which is likely to be confused only with *P. salvadorica. P. neckeroidea* occasionally produces deciduous plantlets on the leaves (e.g. in *Jones* 1408), though more rarely than does *P. salvadorica*.

7. **Plagiochila pectinata** (Willd.) Lindenb., *Sp. hepat.*: 14 (1839); E. Jones in *Trans. Br. bryol. Soc.* **4**: 265 (1962).

SIERRA LEONE. Presumably from near Freetown, *Barter*, two un-named collections in Herb. Mitten (NY), det. Jones.

GHANA. Atewa Hills F.R., on base of a *Gilbertiodendron limba, Richards & Hossain* (GC 36671); on boles of trees in swamp forest (the 'Kaolin Swamp'), *Jones* 1330a.

Plagiochila pectinata is a montane species with a very disjunct distribution. It is abundant in the Mascarenes, in Tanzania in the Uluguru Mountains, and on the islands of the Gulf of Guinea; there are no records from Cameroon. The occurrence of outliers further west is therefore remarkable. In the Atewa Hills, *P. pectinata* is certainly very local, and it is probable that both records come from the same small swamp, where the plant is very abundant. A specimen in the British Museum collected *c.* 1823 by George Don, labelled 'Africa tropica occidentalis' probably came from near Freetown, but as Don also visited São Tomé he may have collected it there. It is likely that, as with *P. barteri*, the destruction of the primary forests has exterminated *P. pectinata*.

8. **Plagiochila pinniflora** Stephani in *Hedwigia* **30**: 212 (1891); E. Jones in *Trans. Br. bryol. Soc.* **4**: 281 (1962).

SIERRA LEONE. Loma Mountains, Sokurela, on branch of tree in swamp forest, *Jones* 1465b.

Jagbahun (8°08′N, 11°56′W), hanging from branches of kola trees, *Deighton* 3083. Gama ['Ngaama'] (7°44′N, 11°13′W), upper branches of tree, *Deighton* 5882. Gola North F.R., on branch of tree in unexploited forest, *Jones* 1571.

GHANA. Oda, on cocoa, *Irvine* 9. Bunso, on cocoa, *Jones* 1317 p.p. Kade A.R.S., in forest, dominant on upper branches of *Aningeria, Hossain* (GC 39316); on branches of *Entandophragma, Richards* 6318. Amedzofe, 730 m (2400 ft), on cocoa, *Jones* 1271.

Plagiochila pinniflora is characteristic of the lowland rain forest of West Africa, and extends into the Congo Basin and western Uganda. It is often abundant in the crowns of trees, and, like other species of this habitat, is rarely collected unless from felled trees or fallen branches. It does, however, also occur freely in plantations, especially of cocoa. In Sierra Leone it may, perhaps, be present chiefly in the south-east. It is a distinctive species which never gives rise to difficulties of identification unless it is very depauperate.

9. Plagiochila praemorsa Stephani in *Bot. Jb.* **8**: 92 (1886 ['1887']); E. Jones in *Trans. Br. bryol. Soc.* **4**: 300 (1962).

SIERRA LEONE. Freetown Peninsula: Leicester Peak, on rock, *Brenan* (*Jones* 478) Sugar Loaf Gap, on understorey shrubs, *Harrington* 648 p.p. Gola Hills: near Lalehun, *Marshall* s.n.; Gola North F.R., on fallen branch in unexploited forest, *Jones* 1570a, and on stem of small undershrub, *Jones* s.n.

GHANA. Krokosua Hills F.R., *c.* 550 m (1800 ft), festooning twigs and boles of trees in seasonally wet forest around a 'glade', slender forms, *Jones* 1404 p.p., 1405. Ankasa River F.R., epiphyllous, *Jeník* (Herb. Jones & OP). 'Ashanti', *Cummins* (G 5165). Tarkwa, *Saxby* (CGE, sub *Plagiochila strictifolia*). Subri F.R., on *Mitragyne* in swamp forest, *Jones* 1356, and on *Raphia* in swamp, *Jones* 1354b. Pra-Suhien F.R., on exposed tree root in bank, *Jones* 1342a, and on bole 1–3 feet from ground, *Jones* 1342b. Ochi Headwaters F.R., *West-Skinn* 187, 193. Begoro, on flat rocks by stream above the waterfall, *Jones* 1311a p.p.; on horizontal bough in open place at foot of waterfall, *Jones* ?1313 (perhaps *Plagiochila strictifolia* forma). Atewa Hills F.R., on small shrubs by stream in deep shade, *Jones* 1324b; clothing the boles of trees in swamp forest (the 'Kaolin Swamp'), slender forms, *Jones* 1330b. Kade A.R.S., on small poles in swamp forest, *Jones* s.n.

Like *Plagiochila neckeroidea, P. praemorsa* is widely distributed in the lowland rain forest of West Africa, and extends into the Congo Basin, usually in sites of high atmospheric humidity. It is extremely variable, and forms occur which are difficult to separate from forms of *P. strictifolia* and *P. fusifera.* It sometimes grows in extremely slender states that would be impossible to name without the evidence of associated more robust shoots. Such forms, mingled with many other bryophytes, clothe the tree boles with a thick mantle in the 'Kaolin Swamp' of the Atewa Hills F.R. (*Jones* 1330b; also s.n.), and they also festoon the twigs of small trees in a piece of wet woodland on the Krokosua plateau.

10. Plagiochila salvadorica Stephani in *Hedwigia* **30**: 272 (1891); E. Jones in *Trans. Br. bryol. Soc.* **4**: 293 (1962).

SIERRA LEONE. Freetown Peninsula: Guma Valley, epiphyte in unexploited forest, *Harrington* 100; Picket Hill, in forest just below the summit, *c.* 850 m (2800 ft), *Gledhill* s.n. Gola North F.R., abundant on the boles of trees, *Jones* 1557, 1559b, 1564, 1569.

GHANA. Ankasa River F.R., on stems of understorey shrubs near the river, *Jones* 1375c. Atewa Hills F.R., very abundant on the boles of large *Lophira* etc., in swamp forest (the 'Kaolin Swamp'), *Jones* 1328; dominant on the trunk of *Gilbertiodendron limba, Richards & Hossain* (GC 36669) (perhaps the same locality as *Jones* 1328).

Plagiochila salvadorica is closely allied to *P. neckeroidea,* and this is the only species with which it is likely to be confused. The two species have a generally similar geographical range, and indeed they sometimes grow together, though in Zaire and in Nigeria (if indeed it occurs) *P. salvadorica* seems to be rare, and *P. neckeroidea* frequent. In the western part of the range *P. salvadorica* is at least as abundant as *P. neckeroidea*. The essential difference between the two species lies in the shape of the postical leaf base – diverging away from the stem close to the insertion in *P. neckeroidea*, but prolonged forwards parallel to the stem for an appreciable distance before bending outwards into the postical margin in *P. salvadorica. P. salvadorica* often, though by no means always, forms deciduous plantlets on the leaves, while *P. neckeroidea* rarely does so; this character cannot be relied on to separate the species.

11. **Plagiochila strictifolia** Stephani in *Hedwigia* **30**: 210 (1891); E. Jones in *Trans. Br. bryol. Soc.* **4**: 297 (1962).

SIERRA LEONE. Freetown Peninsula: Leicester Peak, on tree trunk in rather open forest, *Brenan* (*Jones* 479), on stems of small shrubs, *Jones* 1431 p.p., on base of mango, *Jones* 1461a; Sugar Loaf Gap, on understorey shrubs and small trees, *Harrington* 651. Loma Mountains, forest above Sokurela, 910–1220 m (3000–4000 ft), a slender and probably depauperate plant, named with doubt, *Jones* 1471a. Kambui Hills, Bambawo, on low vegetation in forest, *Harrington* 481.

GHANA. Krokosua Hills F.R., 520–550 m (1700–1800 ft), on stems of small undershrubs, *Jones* 1379b; on liane, *Jones* 1389 p.p. Tarkwa, *Saxby* (CGE). Subri F.R., on base of liane, *Jones* 1357. Atewa Hills F.R., bases of shrubs by stream, *Jones* 1324; bole of *Vernonia*, *Jones* 1325b; at base of stems in swamp forest, *Jones* 1329; stems of understorey shrubs, *Jones* 1293. Kade A.R.S., in swamp forest, *Jones* s.n. Kpedze, on cocoa, *Jones* s.n.

Plagiochila strictifolia is widely distributed and often abundant in the lowland rain forest of West Africa and the Congo Basin, and there are also records for Uganda, Tanzania (Usambara Mountains), and Angola.* It is very variable and some forms are difficult to distinguish from *P. praemorsa*; confusion with forms of *P. fusifera* is also possible. *P. strictifolia* usually grows near the bases of stems quite close to the ground, with other species of *Plagiochila* at higher levels. Thus on an old mango on Leicester Peak, Freetown, *P. strictifolia* grew at the base, with *P. moenkemeyeri c.* one m (3–4 ft) above (*Jones* 1461b). It often grows in deep shade, and often also on the bases of trees close to water (e.g. *Jones* 1324), though not where it is liable to submergence.

XLIV. **PORELLA** L.

1. **Porella subdentata** (Mitten) E. Jones in *Trans. Br. bryol. Soc.* **4**: 456 (1963), var. **subdentata**

SIERRA LEONE. Musaia Agricultural Station, pumping station, *Haswell* B1 p.p. Near road-bridge over tributary of the Rokel River, *c.* 32 km (20 miles) south-west of Kabala, on boulder, *Harrington* 406. Lake Sonfon, on exposed tree roots in forest, *Harrington* 38. Loma Mountains: forest between Kurubonla and Seradu, 610 m (2000 ft), *Jones* 1520a; Seradu, in forest by the village, *Jones* 1516; tree-bough in forest above Sokurela, 1070 m (3500 ft), *Jones* 1467; near 'Camp 1', 1220 m (4000 ft), on boulder, *Harrington* 243, and on tree, *Harrington* 250, 266 p.p.; on sloping rocks and tree boles, very abundant, 1310 m (4300 ft), *Jones* 1508; forest below Dawule, *Morton* (*Harrington* 295a p.p., 295b p.p.); *Jaeger* 1358 (PC).

GHANA. Agogo, *Foote* s.n. Amedzofe, 700 m (2300 ft), above the waterfall on dry rocks and tree boles in deep shade, *Jones* 1275a, b.

var. **camerunensis** E. Jones in *Trans. Br. bryol. Soc.* **4**: 456 (1963).

GHANA. Begoro, draping horizontal bough in open place in forest below the waterfall, *Jones* 1313.

Porella subdentata is widely distributed but local in West Africa; it is usually abundant where it occurs. It is probably the most widely distributed *Porella* in Africa, extending through the Congo Basin to Uganda, Kenya, and Angola. It shows montane tendencies; all the sites listed above are probably near or above 300 m (1000 ft), but it reaches its greatest abundance at moderate altitudes. Thus in the Loma Mountains it is uncommon below 900 m, and abundant in the forest at 1200–1300 m, but has not been recorded from the forest of the plateau at *c.* 1500 m, where it must be rare, if indeed it is present. Probably it does not migrate readily into new habitats, so that freedom from fires and disturbance may play a large part in determining its distribution.

Var. *subdentata* has leaves, lobules, and underleaves that are entire or very weakly dentate, and var. *camerunensis* has leaves which are sharply dentate at the apex and lobules also sharply dentate, some of the teeth being spiniform; it also has broader lobules than the type variety. *Jones* 1313 from Begoro shows that var. *camerunensis* is not a high-altitude form, as might have been deduced from earlier records, but may be a phenotype produced by high atmospheric humidity, combined, perhaps, with good illumination. In their lobules, the Loma Mountain plants are intermediate between the two varieties; the leaf apices are mostly slightly dentate but without the spiniform teeth of var. *camerunensis,* so that they are best assigned to the type variety.

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* All records of *Plagiochila* spp. that are based solely on ancient and scanty herbarium specimens should be accepted with reserve.

XLV. **PRIONOLEJEUNEA** (Spruce) Schiffner

1. **Prionolejeunea grata** (Gottsche) Schiffner in Engl. & Prantl, *Nat. Pflanzenfam.* **1** (3): 127 (1893); Grolle in *Wiss. Z. Friedrich-Schiller-Univ. Jena* **27**: 14 (1978).

Prionolejeunea serrula (Mitten) Stephani, *Sp. hepat.* **5**: 202 (1913); Vanden Berghen in *Revue bryol. lichén.* **39**: 383 (1973).

GHANA. Ankasa River F.R., mixed with *Bazzania decrescens* subsp. *molleri* on tree bole by the river, *Jones* 1372 p.p. Subri F.R., on stipe of *Raphia* in swamp forest, *Jones* 1352 p.p. Begoro, on bole and roots of *Musanga* near the foot of the waterfall, *Jones* 1308. Atewa Hills F.R., on boles of trees in swamp forest, mixed with *Plagiochila praemorsa, Jones* 1332 p.p.

Prionolejeunea grata is widely distributed in tropical Africa, from Madagascar to Tanzania and eastern Nigeria, though apparently very local; it has not hitherto been recorded from further west.

XLVI. **PTYCHANTHUS** Nees

1. **Ptychanthus striatus** (Lehm. & Lindenb.) Nees, *Naturgesch. europ. Leberm.* **3**: 212 (1838); Vanden Berghen in *Résult. scient. Explor. hydrobiol. Bassin Lac Bangweolo & Luapula* **8** (1): 92 (1972).

SIERRA LEONE. Loma Mountains: forest between Seradu and Kurubonla, 610 m (2000 ft), *Jones* 1520d; forest above Sokurela, near 'Camp 1', *c.* 1220 m (4000 ft), on rock, *Jones* 1506, on trees, *Harrington* 252, 265, etc.; forest below Dawule, *Morton* (*Harrington* 295a p.p., 295b p.p.).

Ptychanthus striatus is one of the most characteristic bryophytes of mountain forest throughout tropical Africa, where it often drapes the trunks and branches of trees with its long pinnate fronds. It extends into South Africa, and is widely distributed in the mountains of the Indo-Malayan region.

XLVII. **PYCNOLEJEUNEA** (Spruce) Schiffner

1. **Pycnolejeunea contigua** (Nees) Grolle in *J. Hattori bot. Lab.* **45**: 179 (1979); E. Jones in *J. Bryol.* **10**: 397 (1979).

SIERRA LEONE. Gola North F.R., boughs in crown of large tree, rare and in small patches where no other bryophytes are present, *Jones* 1563.

GHANA. Ankasa River F.R., boughs in crown of *Glutea*, one mile south of the Ankasa bridge, *Jones* 1380a. Atewa Hills F.R., boughs in crown of *Lophira, Jones* 1319d. Aiyaola F.R. near Kade, boughs in crown of large *Piptadeniastrum, Jones* 1234, 1235 p.p.

Pycnolejeunea contigua, originally described from Brazil, has only recently been recognized in Africa, though it is evidently widely distributed in the rain forest. It has doubtless been overlooked and rarely gathered because it grows only on boughs in the crowns of large forest trees where it is inconspicuous, although not a small plant, because it forms small, very closely applied patches of a greyish-green or pale chocolate-brown colour. Moreover it tends to grow where the bryophyte cover is sparse; it was associated in *Jones* 1235 with the moss *Calymperopsis disciformis* (C. Mueller) P. Tixier, and in *Jones* 1319d with *Cheilolejeunea trifaria*.

XLVIII. **RADULA** Dumort.

1. **Radula appressa** Mitten in *Phil. Trans. R. Soc.* **168**: 397 (1879); E. Jones in *J. Bryol.* **9**: 479 (1977).

Radula guineensis Stephani in *Hedwigia* **23**: 133 (1884).

SIERRA LEONE. Loma Mountains, *c.* 1680 m (5500 ft), on *Vernonia* in scrub on the west flank of Bintimani, *Jones* 1499. Giema, on tree in secondary forest, *Harrington* 547. Gola North F.R., on small pole in exploited forest, *Jones* 1561.

GHANA. Pampramasi, on smooth bole of small tree in forest, rare and depauperate, determination uncertain, *Jones* 1408. Ankasa River F.R., base of *Parinari, Richards & Hossain* (GC 36677); base of smooth bole on edge of small gap, *c. per., Jones* 1373a, b. Subri F.R., bole of small tree in *Raphia* swamp, *Jones* 1354. Begoro waterfall, bole of tree in deep shade, *Jones* 1310. Atewa Hills F.R., boughs in crown of *Cassipourea, Jones* 1299b; on bole of *Cassipourea, Richards & Hossain* (GC 36662). Kibi ['Kibbi'], in evergreen forest, *Irvine* 29. Esukawkaw F.R., *Jeník* (OP). Kade A.R.S., amongst *Plagiochila praemorsa* on bole of tree in swamp forest, rare, *Jones* s.n. Osenasi (16 km south-east of Kade), on cocoa, *Jones* s.n.

Radula appressa is the commonest species of corticolous *Radula* in the lowland rain forests of tropical Africa, where it is very widely distributed. If, as is probable, it proves synonymous with *R. javanica* Gottsche, it is also widely distributed in the Indo-Malayan region. It usually occurs in small amounts, however, often mixed with other larger bryophytes. The tough, dark brown stem will usually distinguish it in the field from corticolous forms of *R. flaccida* and from *R. holstiana*; in critical cases the cross section of the stem provides a clear distinction.

2. **Radula boryana** (Fried. Weber) Nees, *Syn. hepat.*: 254 (1845); E. Jones in *J. Bryol.* **9**: 495 (1977).

GHANA. Atewa Hills F.R., very abundant on tree boles in swamp forest (the 'Kaolin Swamp'), *Jones* 1322b; on base of *Gilbertiodendron limba, Richards & Hossain* (perhaps the same locality) (GC 36672 p.p.). Amedzofe, in damp shady position near the waterfall, *Irvine* 416.

Radula boryana is widely distributed throughout the mountains of tropical and South Africa, usually at altitudes of 1200 m and more. It is probably pantropical. The Ghana localities are exceptionally low, though it grows as low as 300 m in the Mascarenes. It doubtless requires high atmospheric humidity.

3. **Radula flaccida** Lindenb. & Gottsche, *Syn. hepat.*: 726 (1847); E. Jones in *J. Bryol.* **9**: 499 (1977).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., epiphyllous, *Harrington* 86 p.p., 87 p.p., 103 p.p., *Jones* 1423 p.p.; York Pass, forest understorey by stream, *Harrington* 613 p.p., 615 p.p. Kasewe F.R., *Richards* R7170 p.p. Kambui Hills, Bambawo, on low vegetation in forest, *Harrington* 442 p.p.; on shrubs in stream gully, *Jones* 1552. Giema, epiphyllous in secondary forest, *Harrington* 512 p.p., 528 p.p., 529 p.p., 532 p.p. Gola Hills: in forest near Lalehun, *Marshall* s.n.; by the river, Lalehun, *Jones* s.n.; Gola North F.R., on herbs in unexploited forest, *Jones* 1568 p.p.

GHANA. Krokosua Hills F.R., 490–550 m (1600–1800 ft), epiphyllous on low shrubs in forest, *Jones* 1396 p.p. Ankasa River F.R., by the river, *Jones* 1375 p.p.; in moist gully, *Richards* R7054; *Jeník* s.n. Aiyinasi, by the river Fiakpole, *Jones* 1364b. Begoro waterfall, *Jones* ! Southern Scarp F.R., *Jones* ! Bunso, on boles of cocoa, *Jones* 1317.

Radula flaccida is the commonest *Radula* in the African lowland rain forest. It is usually epiphyllous, and is one of the most abundant epiphyllous hepatics. It is usually readily recognized in the field by the distinctive large reniform gemmae, which are, however, not invariably present. In their absence, the closely appressed shoots with their regular bipinnate branching and slender green stems help to distinguish it from all except *R. stenocalyx.* It is not uncommon on tree boles and branches, but in this habitat it has usually been either overlooked or misidentified.

4. **Radula ?holstiana** Stephani in *Bot. Jb.* **22**: 320 (1895); E. Jones in *J. Bryol.* **9**: 483 (1977).

SIERRA LEONE. Loma Mountains, western flank of Bintimani, *c.* 1680 m (5500 ft), on *Vernonia* in scrub, *Jones* 1503b.

GHANA. Atewa Hills F.R., on the large branches of a *Cassipourea, Richards & Hossain* (GC 36665); in the crown of a *Cassipourea, Jones* 1299b; in the crown of a *Lophira, Jones* 1319. Aburi Botanical Gardens, on an old *Cycas, Jones* s.n.

All the above specimens are very scanty and sterile, and cannot be named with certainty. The shoots are mingled with Lejeuneaceae and mosses, closely applied to twigs and small branches. They agree with *Radula holstiana* in the structure of the stem. The lobules have a long insertion and are slightly ampliate, but have a very strongly developed rhizoidiferous mamilla, and therefore often a very convex keel. A similar plant has been collected in Guinea in the Macenta Massif by S. Lisowski ('apud flumen Loffa', 25 January 1962, OP). *R. holstiana* is abundant in the East African mountains, and also occurs on Mont Cameroun (Cameroon Mountain), so that on geographical grounds its occurrence in montane situations in Ghana and Sierra Leone is likely. Moreover, *R. holstiana* is the only species of *Radula* with this form of stem and lobule known from West Africa, though others occur in East Africa and the Mascarenes.

5. **Radula stenocalyx** Montagne in *Annls Sci. nat.* (Bot.) IV, **3**: 315 (1855); E. Jones in *J. Bryol.* **9**: 502 (1977).

SIERRA LEONE. Freetown Peninsula, York Pass, forest understorey by stream, *Harrington* 613 p.p., 615 p.p. Masimo, *Marmo* 160 p.p. Kambui Hills, Bambawo, in forest by stream, *Harrington* 440 p.p., 441b, 442 p.p. Gola North F.R., in unexploited forest, *Jones* 1568 p.p.

GHANA. Ankasa River F.R., on leaves of undergrowth in moist gulley near mile 18 from Mpataba, abundant, and often mixed with *Radula flaccida, Richards* R7054. Atewa Hills F.R., by stream in forest, abundant, *Jones* 1294; on leaves of herbs in the 'Kaolin Swamp', abundant, *Jones* s.n.

Radula stenocalyx resembles *R. flaccida* in habit, but differs in the form of the gemmae, which are circular and attached by one edge to the antical margin of the leaf, and in the shape of the lobule; the gemmae are not as freely produced as in *R. flaccida,* and are often inconspicuous. It is a montane species, and usually occurs at higher altitudes than *R. flaccida*; it is unusual to find both species together, though in *Harrington* 613 p.p., 615 p.p. from York Pass, *Harrington* 442 p.p. from the Kambui Hills, *Jones* 1568 from the Gola Hills, and *Richards* R7054 from the Ankasa River F.R. in Ghana both species are mixed on the same leaves. The Ankasa River F.R. is also abnormally low for the occurrence of *R. stenocalyx*.

XLIX. RECTOLEJEUNEA A. W. Evans

1. **Rectolejeunea ?arnellii** E. Jones in *J. Bryol.* **8**: 71 (1974).

SIERRA LEONE. Freetown Peninsula: S. Arnell, in a letter to E. W. Jones dated 31 May 1953, wrote that he had found 'a small specimen of *Rectolejeunea rhodesiae*' amongst his collections from Freetown; he did not publish the record. The relevant packet (in S) is labelled 'Freetown, S. Leo. S. Arnell 20 XII 1951'. It contains only a few fragments of bark-debris amongst which are two minute fragments of a *Rectolejeunea* each bearing two to three leaves. Kabala, near the District Officer's house, on old *Citrus, Jones* 1524d. Kambui Hills, Bambawo, on smooth stem of a small *Drypetes* in young-growth forest near the Rest House, *Jones* 1532c.

In *Jones* 1532c a few stems were scattered in a very mixed sheet of *Archilejeunea africana, Lopholejeunea subfusca, Lejeunea caespitosa, Cheilolejeunea intertexta, Microlejeunea africana,* and *Lejeunea camerunensis*, but they show the deciduous leaves with their uniformly thickened hexagonal cells 20–22 μm diam. and indications of the outgrowths of marginal cells characteristic of the genus; a single perianth was seen. *Jones* 1524d is less mixed but is also a very small gathering; the cells are thinner walled, but it is clearly the same species. The perianths are convex dorsally, not plane as described for East African *Rectolejeunea arnellii* (Jones, *op. cit.*) (and are thus nearer to *R. brittoniae* A. W. Evans), but they have only a very short and low dorsal keel. Neither collection is adequate for certain identification of the species.

Schuster (1980) regards *Rectolejeunea arnellii* as falling within the range of variation exhibited by *R. brittoniae*.

L. RICCARDIA Gray

1. Riccardia angusticosta [‘*angusticostata*’] (Stephani) Grolle in *J. Hattori bot. lab.* **36**: 550 (1972).

Riccardia stephanii (Bescher.) E. Jones in *Trans. Br. bryol. Soc.* **3**: 81 (1956), non S. Hatt. in *Bull. Tokyo Sci. Mus.* **11**: 164 (1944).

SIERRA LEONE. Gola North F.R., on fallen log, *Jones* s.n.

GHANA. Ankasa River F.R., on decaying bark in swampy forest, mixed with *Arachniopsis, Richards* R7061 p.p. Aiyinasi, in forest north of the Agricultural Research Station, on large rotten log, *Jones* 1361c; on rotten log in cut-over forest near the river Fiakpole, *Jones* 1364c. Pra-Suhien F.R., abundant on rotting logs, *Jones* 1339a. Begoro, in forest below the waterfall, on rotting log, *Jones* 1309.

Riccardia angusticosta differs from *R. limbata* in being smaller with branches consisting mostly of unistratose wing, only three cells thick in the middle, while *R. erosa* (Stephani) E. Jones differs in being even smaller. *Jones* 1309 and 1361c both include fronds that are small enough for *R. erosa*, mixed with fronds that are typical *R. angusticosta*; there seems to be no reason for considering these collections to be mixtures of two species. Berrie (1966) found chromosome numbers of $n = 10$, 20, and 40, supplemented by a variable number of chromosome fragments, in a population of *R. stephanii* (= *R. angusticosta*). These observations suggest that *R. limbata, R. angusticosta,* and *R. erosa* are at most varieties of a single species, with much ill-defined intraspecific variation.

2. Riccardia limbata (Stephani) E. Jones in *Trans. Br. bryol. Soc.* **3**: 79 (1956).

SIERRA LEONE. Freetown Peninsula: in forest above Bathurst, 460 m (1500 ft), covering low stone in stream, constantly wet, *Jones* 1433; by stream three km north-east of Toke, covering moist sheltered well-lit rock, *Jones* 1447a & b; near York, *Richards* R7094. Loma Mountains, *c.* 1520 m (5000 ft), moist earth bank of streamlet in shade, *Jones* 1496b. Kambui Hills, Bambawo, steep earth bank by path, *Harrington* 443, 445; damp silt in floor of old mine workings, *Jones* 1542b.

GHANA. Begoro, below the waterfall, in wet well-lit site on tree boles, *Jones* 1308b. Atewa Hills F.R., earth side of old pit, *Jones* 1300. Amedzofe, in shallow pool in very shady rocky spot in waterhole below Gemini, *Irvine* 402 & 421a (sterile; an aquatic form of either *Riccardia limbata* or *R. longispica* (Stephani) E. Jones); on dripping wet cliff in deep shade, in ravine above the waterfall, *Jones* 1280 (sterile).

Much more study of populations in the field is needed before the taxa of the complex that includes *Riccardia limbata* can be satisfactorily delimited. There seems to be little other than habit to differentiate *Riccardia limbata* from *R. longispica*, and little other than size and the lesser development of wings to differentiate it from *R. angusticosta*; both also are very close to *R. multifida* (L.) Gray. Of the plants recorded above, *Jones* 1447a & 1496b, *Richards* R7094 and *Irvine* 402 & 421a might equally well be referred to *R. longispica,* while *Jones* 1300 might equally well be large *R. angusticosta.* Pearson (1931) recorded *Aneura travisiana* Pearson, collected by Saxby from Tarkwa, though he stated that it differed from the type in being less winged and more digitately branched. Jones (1956) considered that the type of *A. travisiana* was *Riccardia stephanii* (= *R. angusticosta*) but that Saxby's plant (Tarkwa, on dead wood, CGE – it has not been possible to trace a specimen at MANCH) was different. The Tarkwa plant may be a xeromorphic form of *R. limbata*, of which it has the dimensions (thallus 0·6–0·8 mm wide, five cells thick in the middle, biconvex in cross section, or, according to Pearson, plano-convex), differing only in the wings being only one cell wide and in the rather irregular subpinnate or more or less palmate branching.

3. Riccardia sp.

GHANA. Between Vane and Amedzofe, rocks in roadside bank, *Jones* 1262. Amedzofe, earth bank near the Training College, *Hall* (GC47071).

Fronds bright green, crowded, imbricate, ascending shoots 2–4 mm long and 0·4–0·5 mm wide, irregularly shortly pinnate, in cross section plane dorsally and convex ventrally or often slightly concave dorsally, thus channelled above, three cells thick and, where not gemmiferous, with a unistratose wing two to three cells broad; usually producing abundant gemmae from the marginal and many cortical cells around the apices of the shoots; gemmae two-celled, 20–28 × 35–40 μm. Median cortical cells (25)–35–45 × 50–60–(95) μm, inner cells of the wings 35 × 55–70 μm, marginal cells 22–30 × 25–35 μm. Oil bodies in all cells, mostly one per cell, occasionally two or three, dark grey, opaque, granular, oval with rounded or occasionally pointed ends, those in the cortical cells 8 × 10–14 μm, in the medullary cells 9 × 24–30 μm. Only male plants seen.

Jones kept GC 47071 (kindly sent by air mail by Mr J. B. Hall) in cultivation at Kirtlington for two years. It produced copious male inflorescences but no female, so that there is little doubt that it is a dioecious species. It produced few gemmae in cultivation, and continued to make prostrate pinnate shoots with narrow parallel-sided fronds.

What is apparently the same species has been collected by De Sloover (13338, NAM) in the Forêt de Gishwati, Rwanda, by Demaret (6471, BR) at Yaselia in the Parc National Albert of the former Belgian Congo, and in Mauritius by Vaughan (MAU 11730); *De Sloover* 13338 is female. The plant from Mauritius has also been cultivated at Kirtlington, and like that from Amedzofe it is persistently male.

It is tempting to name this species *Riccardia incurvata* Lindb., though the geographical distribution of *R. incurvata*, so far as it is known at present, makes this identity improbable. European *R. incurvata* differs chiefly in having a thallus five to six cells thick, with the contrast in size between cortical and medullary cells less pronounced; it is also more consistently lunate in cross section.

LI. **RICCIA** L.

1. **Riccia fluitans** L., *Sp. pl.*: 1139 (1753); Vanden Berghen in *Résult. scient. Explor. hydrobiol. Bassin Lac Bangweolo & Luapula* **8** (1): 186 (1972).

GHANA. Nsuta, in the Pra River, *Jones* !

Riccia fluitans is frequent throughout Africa in fresh water, and will doubtless prove to be widely distributed in both Sierra Leone and Ghana.

2. **Riccia lanceolata** Stephani in *Hedwigia* **27**: 110 (1888); E. Jones in *Trans. Br. bryol. Soc.* **3**: 218 (1957).

GHANA. Near Kumasi, on an inselberg at mile 13 on the Mampong road, *S. R. Woodell,* June 1971 (Herb. Jones).

Riccia lanceolata is frequent on thin earth over rocks in the southern savannas of Nigeria, and is likely to be frequent in similar situations in Ghana. The spores of the Kumasi plant differed from those described by Jones (*op. cit.*) in being larger (90–100 μm diam.), and in having the outer face areolate over the whole of its surface.

3. **Riccia membranacea** Gottsche & Lindenb., *Syn. hepat.*: 608 (1846); E. Jones in *Trans. Br. bryol. Soc.* **3**: 210 (1957).

GHANA. Nsuta, banks of the Pra River, on heavy rich clay in the flood zone, *Jones* 1351.

Riccia membranacea is widely distributed in tropical Africa on ground that is liable to inundation by rivers, and will doubtless be frequent in both Sierra Leone and Ghana.

4. **Riccia moenkemeyeri** Stephani in *Bot. Jb.* **8**: 95 (1886 ['1887']); E. Jones in *Trans. Br. bryol. Soc.* **3**: 211 (1957).

Riccia undulata S. Arnell in *Bot. Notiser* **105**: 307 (1952).

SIERRA LEONE. Freetown, streamside, *Arnell* 2252 (as *Riccia undulata*). Musaia, in very damp beds of forest nursery, *D. Small* 272, September 1951. Koinadugu village, on bare ground, *Sellar* B46.

GHANA. Cape Coast (5°06′N, 1°15′W), mud near stream, *Hall* 1536. Mpraeso Scarp, probably this species (sterile), in ditch mixed with *Notothylas decurva,* in damp forest, *Hall* 2630.

According to the description provided by Arnell (*op. cit.*), *Riccia undulata* differed from *R. moenkemeyeri* only in its greater size (thallus up to seven mm wide). The type specimen in S is much smaller, and well within the normal range of size of *R. moenkemeyeri*; the spores are identical with those of *R. moenkemeyeri.*

Riccia moenkemeyeri is widely distributed in tropical Africa from Nigeria eastwards into the Congo Basin. It has also been recorded from Gambia (rice fields near Keneba, *D. H. Murphy,* 30 December 1958, BM). Belonging to the subgenus *Ricciella*, it tends to occur in wetter country than most species, which belong to the subgenus *Riccia,* and is frequent in rain forest districts.

5. **Riccia nigrosquamata** E. Jones in *Trans. Br. bryol. Soc.* **3**: 222 (1957).

SIERRA LEONE. Freetown Peninsula, on laterite soil by the Fourah Bay College Guest House, *G. K. Berrie* s.n., August 1971 (Herb. Jones). Musaia town, on house foundation, *Donald* s.n. Koinadugu village, on bare ground, *Sellar* B48.

Riccia nigrosquamata is known from Tanzania and from the neighbourhood of Ibadan in Nigeria; it is to be expected in Ghana.

6. **Riccia rhodesiae** S. Arnell in *Bot. Notiser* **105**: 313 (1952); E. Jones in *Trans. Br. bryol. Soc.* **3**: 220 (1957).

GHANA. Kibi ['Kibbi'], evergreen forest, *Irvine* 29. Achimota College, in lawn, *Boughey* (Herb. Jones). Legon University, in the Botanical Gardens, and in turf around the Botany Department, *Jones* 1386.

LII. RICCIOCARPOS Corda

1. **Ricciocarpos natans** (L.) Corda in Opiz, *Beitr. Naturgesch.*: 651 (1829); Vanden Berghen in *Résult. scient. Explor. hydrobiol. Bassin Lac Bangweolo & Luapula* **8** (1): 184 (1972).

GHANA. Dabala, near Sogakofe, Lower Volta (5°59′N, 0°41′E), in newly flooded swamp, with *Azolla, Salvinia,* etc., *Hall* B10.

Widely distributed in fresh water throughout tropical and temperate regions.

LIII. SCHIFFNERIOLEJEUNEA Verd.

1. **Schiffneriolejeunea fragilis** Gradst. & E. Jones in *J. Bryol.* **12**: 45 (1982).

SIERRA LEONE. Loma Mountains, Seradu, on boles of trees in forest by the village, *Jones* 1515a, 1516a, 1517. Kambui Hills, Bambawo, bole of tree in forest near the Rest House, *Jones* 1550b.

GHANA. Kade A.R.S., on main trunk and branches of *Aningeria, Hossain* (GC 39306, 39318 *et al.*); on upper branches of *Parinari, Hossain* (GC 36700, 39339).

Schiffneriolejeunea fragilis is the plant alluded to by Jones (1954*a*: 400) as allied to *Ptychocoleus pappeanus* (Nees) Stephani (= *Schiffneriolejeunea pappeana* (Nees) Gradst. in *J. Hattori bot. Lab.* **38**: 335 (1974)). It is a species of the lowland rain forest of West Africa and the Congo Basin, in contrast to *S. pappeana,* which occurs in South Africa and the mountains of tropical Africa, including Mont Cameroun (Cameroon Mountain).

2. **Schiffneriolejeunea occulta** (Stephani) Gradst. in *J. Hattori bot. Lab.* **38**: 333 (1974).

Ptychocoleus occultus (Stephani) Stephani, *Sp. hepat.* **5**: 25 (1912); Vanden Berghen in *Bull. Jard. bot. Etat Brux.* **19**: 47 (1948).

SIERRA LEONE. Freetown Peninsula: Mount Aureol, *Arnell* 2309, 2328; Fourah Bay College B.R., near Heddle's Farm, on bole of tree with *Marchesinia excavata, Jones* 1420 p.p.; Toke, in scrub behind the beach, on boles of *Terminalia scutifera* and *Chrysobalanops, Jones* 1444b, 1446b; Black Johnson Beach near York, in thicket behind the beach, *Harrington* 22. Rokupr, West African Rice Research Station (9°01′N, 12°57′W), *c.* 15 m (50 ft), on tree buttress, *Harrington* 77. Njala, upper part of trunk of *Nauclea diderrichii, Deighton* 5313 p.p. Jawo, near Kenema, smooth bole of tree on bank of the river Moa, *Jones* 1538a.

GHANA. Aiyinasi A.R.S., on *Citrus, Jones* 1383.

Schiffneriolejeunea occulta is known elsewhere from the lowland rain forest of western and eastern Nigeria, and the Congo Basin.

3. Schiffneriolejeunea polycarpa (Nees) Gradst. in *J. Hattori bot. Lab.* **38**: 335 (1974).

Ptychocoleus molleri (Stephani) Stephani, *Sp. hepat.* **5**: 29 (1912); Vanden Berghen in *Bull. Jard. bot. État Brux.* **19**: 44 (1948).

SIERRA LEONE. Freetown Peninsula: Havelock Plateau, on branches of bushes in scrub, *Jones* s.n.; Leicester Peak, 460 m (1500 ft), on old mango below the Rest House, *Jones* 1464b p.p., in evergreen scrub, 520 m (1700 ft), *Jones* 1457f, in both collections mixed with *Acrolejeunea emergens* var. *confertissima*. Five km south of Kabala, in secondary forest, *Harrington* 120. Kabala, near the District Officer's bungalow, on mango, *Harrington* 133, 140 p.p. Lake Sonfon, on *Erythrophleum* near stream, *Harrington* 28 p.p., 29 p.p., 52 p.p. Loma Mountains, Seradu, in forest by the village, on tree boles mixed with *Schiffneriolejeunea fragilis, Jones* 1515c. Kambui Hills, Bambawo, on large tree by road, *Harrington* 569 p.p.

GHANA. Kade A.R.S., in crown of *Entandophragma, Richards* R6307 – probably this species, but determination uncertain as the female inflorescences are all eroded and the male not found. Aburi Botanical Gardens, on roots of *Hura crepitans,* and on bole of cabbage palm, *Jones* s.n. Amedzofe, 'on tree trunks in cloud forest', *Irvine* 412 p.p.; on shade tree in old coffee farm, 730 m (2400 ft), *Jones* 1245.

Schiffneriolejeunea polycarpa extends from Guinea to Natal and the Mascarenes, but its main area of distribution seems to be the Congo Basin and the Tanzanian mountains, where it is frequent at altitudes of 800–1700 m. It is also known from tropical America.

LIV. SPRUCELLA Stephani

1. Sprucella succida (Mitten) Stephani in *Hedwigia* **30**: 214 (1891); Vanden Berghen in *Bull. Jard. bot. État Brux.* **18**: 91 (1946).

SIERRA LEONE. Freetown Peninsula: Fourah Bay College B.R., clay bank by path, *Harrington* 595, *Jones* !; Charlotte Falls, bank by road above the falls, *Harrington* 640 p.p. Lake Sonfon, dry watercourse, *Harrington* 51 p.p. Loma Mountains: near 'Camp 1', 1220 m (4000 ft), stream bank in forest, *Harrington* 268; walls of small cave in plateau grassland, south-west of 'Camp 2', 1520 m (5000 ft) *Harrington* 172; western flank of Bintimani, moist earth bank of streamlet, in shade, *Jones* 1496 p.p. Kambui Hills, Bambawo, on termite mound in forest, *Harrington* 413; on earth bank by path near the upper bungalows, *Harrington* 561, *Jones* 1529 p.p.

GHANA. Ankasa River F.R., covering bole of *Vitex* to height of a metre, *Jones* 1370; log by the river, *Richards* R7049. Tarkwa, *Saxby* (CGE). Subri F.R., *Jones* ! Pra-Suhien F.R., abundant, *Jones* ! Begoro, abundant on shady wet rocks below the waterfall, *Jones* 1308 p.p. Near Kibi ['Kibbi'], *Irvine* 31. Atewa Hills F.R., abundant on ironstone rocks on the plateau, *Jones* ! Amedzofe, shady cliff just below the summit of the hill, *Jones* s.n.; bank near the Training College, *Hall* (GC 47071 p.p.).

Sprucella succida is widely distributed in the lowland rain forest of West Africa and the Congo Basin, where it often covers shady banks of moist earth or rock in thick sheets; it also occurs on tree boles and on decaying wood. It extends eastwards into Uganda (East Mengo, *K. A. Lye* B1, Herb. Jones). It is not a montane species, and its occurrence on the Loma plateau at *c.* 1500 m is surprising.

LV. STICTOLEJEUNEA (Spruce) Schiffner

1. Stictolejeunea balfourii (Mitten) E. Jones in *J. Bryol.* **9**: 50 (1976).

Stictolejeunea africana Vanden Berghen in *Bull. Jard. bot. État Brux.* **20**: 15 (1950).

GHANA. Krokosua Hills F.R., 490 m (1600 ft), on liane, *Jones* 1392b, and on tree roots in deep shade, *Jones* 1395. Ankasa River F.R., *Jones* s.n. (GC); on base of *Parinari glabra, Richards* (GC 36677 p.p.). Pra-Suhien F.R., on side of tree root in deep shade, *Jones* 1343a. Kade A.R.S., in forest in deep shade on roots of trees, bases of smooth boles and old lianes, abundant, *Jones* 1217, 1219.

Stictolejeunea balfourii has been rarely collected, but is widely distributed and probably frequent in the lowland rain forest of West Africa and, as it was first described from the Island of Rodrigues, it probably extends throughout the Congo Basin. It is certainly frequent in parts of Bendel State, Nigeria, and in Ghana. It makes thin, very closely applied patches on smooth bark, of a blackish green with a characteristic oily appearance which, once recognized, is unmistakable, but it would be passed over as one of the *Archilejeunea* spp. amongst which it often grows. It usually grows very close to the ground.

LVI. **STREPSILEJEUNEA** (Spruce) Schiffner

1. **Strepsilejeunea brevifissa** (Gottsche) Stephani, *Sp. hepat.* **5**: 275 (1913); Vanden Berghen in *Bull. Soc. r. Bot. Belg.* **92**: 136 (1960).

SIERRA LEONE. Loma Mountains: above Sokurela, 940 m (3100 ft), on tree near lower edge of the forest, *Jones* 1512; gallery forest in centre of plateau, on large branch, *Morton* (*Harrington* 374 p.p.); near 'Camp 2', *c.* 1650 m (5400 ft), on tree on edge of gallery forest, *Harrington* 146; on liane in open place near 'Camp 2', *Jones* 1495; 'sur rameaux d'Eugenia, forêt relique d'altitude vers 1850 [sic] m', *Jaeger* 1188 p.p. (PC).

Strepsilejeunea brevifissa is widely distributed in the African mountains from Madagascar, the Mascarenes, and the Cape to Mont Cameroun (Cameroon Mountain); it has not hitherto been reported from further west. In tropical Africa it occurs from *c.* 1000 to 2500 m, usually straggling amongst other bryophytes on trees. It has often been collected accidentally, so that the specimens which are available in herbaria are mostly scanty. It is extremely variable, particularly in respect of the leaf apex, which may vary from rounded to acuminate, and the carination of the perianth. Gottsche (1882) described the perianths of the original collection from Madagascar as having 'ventre carina lato (fructu maturo fere evanescente) notato'; such plants occur not only in Madagascar but also in East Africa; at maturity the perianth may be pyriform, terete, and completely eplicate. Plants with quinqueplicate perianths that are bicarinate ventrally are frequent, and every intermediate condition between this and the eplicate perianth occurs. Plants on Mont Cameroun have a triplicate perianth with a deep narrow ventral keel. The Loma Mountain plants have quinqueplicate perianths with two long well-defined ventral keels. It is not clear how much, if any, of this variation is genotypic; that it is not entirely due to age is shown by the fact that the perianths of e.g. *Harrington* 146 remain distinctly carinate even when the sporangia have discharged.

LVII. **SYMPHYOGYNA** Nees & Montagne

1. **Symphyogyna lehmanniana** Montagne & Nees, *Syn. hepat.*: 483 (1846); Vanden Berghen in *Résult. scient. Explor. hydrobiol. Bassin Lac Bangweolo & Luapula* **8** (1): 152 (1972).

SIERRA LEONE. Loma Mountains, *c.* 1520 m (5000 ft), on moist earth bank of streamlet in deep shade, mixed with *Riccardia limbata* and *Calypogeia fissa, Jones* 1496 p.p.

GHANA. Amedzofe, steep dripping cliffs near the waterfall, in deep shade, *Irvine* 417 (named with doubt).

Vanden Berghen (1965) found that *Symphyogyna lehmanniana* and *S. volkensii* Stephani differed chiefly in dimensions, *S. volkensii* being a larger plant, and suggested that more copious material might show that the two should be treated as synonymous. He described the central strand of small cells in *S. lehmanniana* in transverse section as 75–120 × 60–90 μm, and consisting of 45–60 cells, that of *S. volkensii* as 50–110 × 80–100 μm, and consisting of *c.* 30 cells. However, an original specimen of *S. lehmanniana* (leg. *Lehmann*) in BM has a central strand only 40 μm broad, consisting of only 30 cells in section. Vanden Berghen recorded *S. lehmanniana* only from South Africa, and *S. volkensii* from Kilimanjaro and Zaire at altitudes of 2500 m upwards.

The Loma plant, *Jones* 1496 p.p., agrees in dimensions with *Symphyogyna lehmanniana*, and though it has a small central strand only 50–70 μm broad × 45–50μm deep, composed of 25–30 cells in section, this is clearly within the range of variation of *S. lehmanniana*. *Irvine* 417 from Ghana is sterile and badly preserved and cannot therefore be named with certainty. It may be

Pallavicinia lyellii (Hook.) Carruth., which is, however, not yet known with certainty from West Africa, whereas *S. lehmanniana* is known from Cameroon (*Richards* R5297 p.p., Bamenda–Banso road, 1675 m). A plant from Mont Cameroun (Cameroon Mountain), with its much greater rainfall (*Jones* 411, 1890 m alt., also leg. *Savory*, 1830–2130 m alt.) differs in having an even smaller central strand, in section of only 15 cells which are thin walled. It should probably be considered as being a hygromorphic form rather than a different taxon.

Grolle (1980: 330) regards *Symphyogyna lehmanniana* as being identical to the neotropical *S. brasiliensis* Nees & Montagne.

LVIII. **TARGIONIA** L.

1. **Targionia hypophylla** L., *Sp. pl.*: 1136 (1753); Vanden Berghen in *Résult. scient. Explor. hydrobiol. Bassin Lac Bangweolo & Luapula* **8** (1): 164 (1972).

GHANA. Mole Game Reserve, *Hall (*GC 47203).

Targionia hypophylla is widely distributed throughout those parts of tropical Africa which have a long severe dry season, growing especially on the banks of watercourses where it is liable to temporary inundation or kept moist by seeping water in the wet season. It is likely to be frequent in northern Ghana, and is to be expected in northern Sierra Leone.

LIX. **TAXILEJEUNEA** (Spruce) Schiffner

1. **Taxilejeunea conformis** (Nees & Montagne) Stephani, *Sp. hepat.* **5**: 456 (1913); E. Jones in *Trans. Br. bryol. Soc.* **5**: 294 (1967).

Lejeunea conformis Nees & Montagne in *Annls Sci. nat.* (Bot.) II, **19**: 260 (1843).

SIERRA LEONE. Loma Mountains: forest near 'Camp 1', 1220 m (4000 ft), *Harrington* 256 p.p.; valley-head west of Bintimani, 1680 m (5500 ft), epiphyllous in scrub, *Jones* 1498a.

GHANA. Amedzofe, in ravine above the waterfall below dripping cliff in deep shade, on rocks, *Jones* 1285a, and epiphyllous, *Jones* 1285b.

Taxilejeunea conformis is widely distributed in the wetter parts of tropical Africa. It is somewhat montane, and is usually found at altitudes of 1000–1600 m.

2. **Taxilejeunea pulchriflora** Pearson in *Ark. Bot.* **19** (5): 15 (1925); E. Jones in *J. Bryol.* **9**: 50 (1976).

SIERRA LEONE. Freetown Peninsula: valley above Kongo Dam, Bathurst, 490 m (1600 ft), on barkless rotten log in forest, *Jones* 1434b p.p. Loma Mountains, valley to west of Bintimani, *c.* 1520 m (5000 ft), on *Cyathea, Jones* 1492 (form with obtuse leaves and no subgynoecial innovations). Kambui Hills, Bambawo, on shaded stonework beneath bridge, *Harrington* 562 p.p. Gola North F.R., on bole of *Vitex,* with *Lejeunea confusa* in cushions of *Calymperes lonchophyllum* Schwaegr., *Jones* 1558 (form with obtuse leaves).

GHANA. Pra-Suhien F.R., on tree root in bank, *Jones* 1340. Southern Scarp F.R., near Begoro, on boulder, *Hall* (*Jones* 1316).

Taxilejeunea pulchriflora is widely distributed in West and East Africa but local, and rarely, if ever, abundant. It is to be expected in the Amedzofe district of Ghana, as it has been collected only a short distance to the east in Togo (Campement de Klouto, 720 m, on sandstone, *Hiepke & Schultze-Motel* 464, B).

LX. **TELARANEA** Spruce ex Schiffner

1. **Telaranea nematodes** (Gottsche ex Austin) M. Howe in *Bull. Torrey bot. Club.* **29**: 284 (1902).

SIERRA LEONE. Loma Mountains, head of the Kongbundu Valley, north-west of Bintimani, *c.* 1520 m (5000 ft), on vertical banks of moist humic earth in grassland, mixed with *Calypogeia longifolia, Jones* 1502 p.p. Kambui Hills, Bambawo, on steep shaded earth bank, *Harrington* 445 p.p.

GHANA. Tarkwa, on rotting wood, *Saxby* (CGE). Atewa Hills F.R., on base of *Gilbertiodendron limba, Richards & Hossain* (GC 36673); on very large fallen rotting tree bole, *Jones* 1321.

Telaranea nematodes is widely distributed but local in tropical Africa. It is to be expected in the Amedzofe district, as, like *Taxilejeunea pulchriflora,* it has been collected a short distance to the east in Togo (between Palimé and Klouto, 650–750 m, *Hiepke & Schultze-Motel* 409, and on the walls of Château Vialle, 750 m, *Hiepke & Schultze-Motel* 427, in both mixed with *Sprucella succida,* B).

LXI. **THYSANANTHUS** Lindenb.

1. **Thysananthus spathulistipus** (Reinw., Blume & Nees) Lindenb., *Syn. hepat.*: 287 (1845); Vanden Berghen in *Revue bryol. lichén.* **19**: 35 (1950).

Lejeunea triquetra Mitten in *J. Proc. Linn. Soc.* **7**: 167 (1863 ['1864']).
Mastigolejeunea tarkwana Pearson in *Annls Cryptog. exot.* **4**: 63 (1931).

SIERRA LEONE. Bagru ['Bagroo'] River, *Mann* s.n. (BM, isotype of *Lejeunea triquetra*).
GHANA. Ankasa River F.R., on bole of tree by the rapids, *Jones* 1376a; in crown of *Glutea* on bole and larger branches, *Jones* 1378b. Tarkwa, *Saxby* (CGE, isotype of *Mastigolejeunea tarkwana*).

Thysananthus spathulistipus, a species widely distributed in the Indo-Malayan region, has also been recorded from Cameroon (Augier, 1978), Nigeria, Zaire, Madagascar, the Mascarenes (Vanden Berghen, *op. cit.*), and Seychelles (Grolle, 1978). The scarcity of records from West Africa may be due partly to the fact that it usually occurs in the crowns of large trees. It is probably confined to 'old-growth' forest.

LXII. **TRACHYLEJEUNEA** (Spruce) Schiffner

1. **Trachylejeunea serrulata** Stephani, *Sp. hepat.* **5**: 300 (1913).

GHANA. Ankasa River F.R., epiphyllous, *Jeník* s.n.; on low shrubs near the river, *Jones* 1375, 1381; on undergrowth in moist gully near mile 18 from Mpataba, *Richards* R7054; on palm leaves in swamp a mile south of the Ankasa bridge, *Jones* 1382d.

This species, hitherto known only from Cameroon, is evidently abundant in the Ankasa River district. The numerous, conspicuous, often reddish ocelli, scattered throughout the leaves, underleaves, and perianths, make it easily recognisable. It is probably wrongly placed in the genus *Trachylejeunea*; Dr R. Grolle (pers. comm.) considers it to be a *Lepidolejeunea*.

LXIII. **TYLIMANTHUS** Mitten

1. **Tylimanthus ?ruwenzorensis** S. Arnell in *Ark. Bot.* II, **3**: 560 (1957); E. Jones in *J. Bryol.* **11**: 317 (1980).

GHANA. Subri F.R., in swamp forest on stipe of *Raphia, Jones* 1352. This plant was sterile and only a very small amount was found, so that identification of the species is impossible.

The genus includes few species. Its occurrence in West Africa at a low altitude is of considerable interest, as hitherto it has been found in tropical Africa only at much higher altitudes in the mountains of the east.

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Y. M. Chamberlain*

The Marine Laboratory, Portsmouth Polytechnic, Ferry Road, Hayling Island, PO11 0DG

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Synopsis

Fosliella M. Howe and *Pneophyllum* Kütz. are simple, calcified crustose, red algae of the family Corallinaceae, subfamily Mastophoroideae. The taxonomy of the genera and the systematics of the species occurring in the British Isles are investigated, based on the analyses of historical publications and herbarium specimens, morphological and anatomical examinations under the scanning electron and light microscopes, observations on spore germination and segmentation, crust growth, and reproduction in laboratory culture, and general and sequential shore observations.

A reinvestigation and reappraisal of the taxa which were known variously as *Heteroderma* and *Fosliella* has resulted in a redefinition of the genera with consequent nomenclatural changes. The genera are now principally distinguished as follows: *Fosliella* – with terminal trichocytes only and a four-celled central element to the germination disc; *Pneophyllum* (= *Heteroderma* Foslie *pro parte*) – with mainly intercalary trichocytes (when present) and an eight-celled central element to the germination disc. The type species, *P. fragile*, possibly from Yugoslavia, is described here in detail for the first time.

Of the twelve British representatives discussed here *Fosliella farinosa, Pneophyllum confervicolum, P. lejolisii, P. limitatum,* and *P. zonale* have been recorded previously; *P. microsporum, P. myriocarpum,* and *P. sargassi* are new records, and *P. concollum, P. lobescens, P. plurivalidum,* and *P. rosanoffii* are newly described. All the British representatives of *Pneophyllum* are new combinations, apart from the new species. Four of these species are epilithic; *P. lejolisii* grows almost exclusively on *Zostera marina*; and the remaining species occur mostly on red and brown algae and often show consistent host preferences. Most epiphytic species occur in greatest abundance in autumn and early winter. Species diversity and abundance is, in general, greater in south and south-west England and Ireland than elsewhere.

Introduction

Members of the marine red algal family Corallinaceae are characterised by their cell walls being impregnated with calcium carbonate, principally in the form of calcite, giving the thallus a hard, rigid texture. As Johansen (1981) remarks, they can be considered as the corals of the plant world. One result of this feature is that these algae, in particular the crustose forms, are especially difficult to collect and investigate. Consequently, until recently, they have been neglected in comparison with most algal groups. On the other hand, the hard thallus means that corallines have fossilised well, and they are thus one of the few macroalgal groups to have a well documented fossil history (cf. J. H. Johnson, 1961; Lemoine, 1970; Wray, 1971; Adey and Macintyre, 1973; Poignant, 1977). A maastrichtian fossil of *Pneophyllum,* preserved by bioimmuration, has recently been described by Voigt (1981, as *Fosliella inexspectata*); this 75 million year old fossil bears a striking resemblance to some present-day forms of *Pneophyllum*.

There are three principal growth forms in the Corallinaceae, all of world-wide distribution, representing three levels of morphological complexity (Cabioch, 1972; Chamberlain, 1978). These are: a) the simple crust, b) the complex crust, and c) the articulated form in which joints (genicula) of uncalcified cells develop between calcified thallus segments (intergenicula).

Corallines constitute an important and conspicuous element in the marine algal flora of the British Isles, where species of the complex crustose genera *Lithothamnion* Heydrich, *Phymatolithon* Foslie, *Leptophytum* Adey, and *Lithophyllum* Philippi cover many intertidal and subtidal rocks with their pink and purple crusts: these crusts have been investigated recently by Adey & Adey (1973). The articulated genera *Corallina* L. and *Jania* Lamouroux are also abundant and members of these and a third articulated genus *Haliptilon* (Decaisne) H. Johansen have been recorded frequently from the British Isles over the years.

The first growth form, the simple crust, produces small, thin, inconspicuous crusts which are mainly epiphytic on other algae and sea-grasses (marine angiosperms), but also occur on shells, rocks, pebbles, and glass fragments. The British genera included in this group are *Pneophyllum* Kütz., *Fosliella* M. Howe, *Dermatolithon* Foslie, and *Melobesia* Lamouroux, as well as a parasitic species, *Choreonema thuretii* (Bornet) Schmitz. An endophytic species formerly thought to belong to this group, *Schmitziella endophloea* Bornet & Batters, has recently been transferred from the Corallinaceae (Woelkerling & Irvine, 1982).

The simple coralline crusts have received scant attention in the British Isles, despite the fact that they occur relatively commonly on many of the shores recognised as being generally rich in algal species. One reason for their neglect may be that they are most abundant during autumn and winter, which are not the most popular seasons for shore collecting. Another reason is that two or more species frequently occur on the same substratum and, since most species possess three distinct reproductive phases (gametangial, tetrasporangial, and bisporangial), it is often difficult to isolate and identify their individual crusts.

The present study was undertaken in order to distinguish and identify British species of simple crustose corallines belonging to the subfamily Mastophoroideae. This firstly necessitated an analysis of vegetative and reproductive characters in the subfamily, leading to a reappraisal of generic distinctions. It was concluded that two genera, *Fosliella* and *Pneophyllum*, were present. One species of *Fosliella* and eleven of *Pneophyllum* were subsequently identified. Although little was known previously about this group in the British Isles, a number of studies on European species are available, and initial identifications were made on the basis of these publications. These include, particularly, works by Lamouroux (1812, 1816), Kützing (1843, 1845, 1849, 1869), the Crouan brothers (1859, 1867), Rosanoff (1866), Foslie (especially 1905*a*), Rosenvinge (1917), Suneson (1937, 1943), Hamel & Lemoine (1953), and Bressan (1974). As the more recent authors had not examined type material described by earlier authors, the nomenclature of the taxa had become particularly confused; type and other historical specimens were, therefore, specially examined in the present study.

Classical algal taxonomy was based almost entirely on morphological and anatomical features. However, the new techniques which have become available in recent years have meant that additional characters have assumed importance, some of which have been utilised in the present study. Investigations on spore germination, crust growth, and reproductive cycles have been carried out on plants grown in running sea-water in the laboratory, and, while details of these investigations are to be published elsewhere, the taxonomic implications of the results obtained are important in the present context. The results obtained from morphological and anatomical investigations, however, still form the basis of species delimitation and, in addition to examining decalcified crusts under the light microscope, calcified crusts have been investigated under the scanning electron microscope. This has both revealed new features of systematic significance and enabled reinterpretation and assessment of features seen previously only in the decalcified state.

Finally, shore collections were made throughout the British Isles to study the geographical distribution of the species, while sequential shore collections were made at the southern English localities of Bembridge, Kimmeridge, and Beer (Chamberlain, 1982). This revealed details of seasonal and ecological patterns of occurrence and led to an appreciation of the variability of the plants and consequent identification problems. The relevant results from this study are incorporated in the species descriptions, while details of the shore observations will be published elsewhere.

The present study commences with a detailed consideration of historical publications on simple crusts, because nomenclatural problems have arisen from previously incomplete analyses of works such as those of Kützing (1843–1869), the Crouan brothers (1859, 1860, 1867), and Rosanoff (1866). The principal features of coralline structure, particularly with regard to the simple crusts, are then described and subsequently used as a basis for discussing the division of the family into subfamilies and genera. Finally, generic and species descriptions of 14 taxa occurring in the British Isles are presented, together with a description of *Pneophyllum fragile* which is the type species of its genus. The summary given at the end of each section follows the precedent set by Hillis-Colinvaux (1980) which I found particularly helpful.

This study is based on material presented for a Council for National Academic Awards Ph.D. thesis (Chamberlain, 1982).

Abbreviations

HERBARIA:
BM = British Museum (Natural History)
BM-K = Royal Botanic Gardens, Kew (algae now amalgamated with BM collection)
C = Botanical Museum, Copenhagen
CHE = Société des Sciences Naturelles et Mathématiques de Cherbourg
CN = Université de Caen
CO = Laboratoire Maritime, Concarneau
DBN = Irish National Herbarium, Dublin
E = Royal Botanic Gardens, Edinburgh
GL = The University, Glasgow
L = Rijksherbarium, Leiden
PC = Muséum national d'histoire naturelle, Paris (Cryptogams)
TRH = Kongelige Norske Videnskabers Selskab Museet, Trondheim (= Nidros)
USNC = United States National Museum Coralline Collection, Washington, D.C.

farctate = this term is used (as by Kützing, 1843) to describe the stuffed, bulging appearance of mature, coralline tetrasporangia.
S.E.M. = scanning electron microscope (Scanning electron micrographs are of air-dried material unless critical point dried material is specified).
VS = vertical section.
! = specimen seen.

Material and methods

Introduction

Four main types of methodology have been used in the present investigation: light microscopy, scanning electron microscopy, sequential field observations, and laboratory culture. Investigations into the morphology and anatomy of the species of *Pneophyllum* and *Fosliella* were based mainly on field-collected and laboratory-cultured material, while herbarium material was examined mainly in relation to typification. Field-collected material was examined while fresh when possible, otherwise, after preservation, in 4% neutralised formalin seawater.

Light microscopy

Since it was not usually possible to identify species of *Pneophyllum* and *Fosliella* on the basis of macroscopic features alone, whole mount and sectioned preparations were examined under a light microscope. When identifying crusts on which to base field observations, slides were prepared using either calcified or declacified whole crusts. Crusts were decalcified by placing them in Perenyi's fluid (4 parts 10% nitric acid: 3 parts 90% ethanol: 3 parts 0·5% chromic acid) until bubbling ceased (this takes only 1–2 minutes in thin species). The calcified or decalcified crust was mounted on a microscope slide in 33% glycerine coloured with lactophenol aniline blue and the mountant allowed to evaporate gradually; eventually the remaining glycerine was drained off and the crust mounted in glycerine jelly coloured with crystal violet.

Routine sectioning of fresh or formaldehyde-preserved material was performed using an MSE Pelcool freezing microtome at a thickness of 10–25 μm. For this purpose epiphytic crusts were decalcified while still on the host; they were then soaked in 70% alcohol for at least 15 minutes and sectioned in Hamilton's freezing solution (1 g gum arabic : 30 g sucrose : one crystal of thymol : 100 ml aqua dest.). The sections were transferred to a microscope slide with a fine paint brush, then mounted in glycerine and finally glycerine jelly as before. Epilithic crusts were usually too flimsy to section unsupported by a host: decalcified crusts were, therefore, attached to a piece of brown seaweed with Hamilton's solution before being frozen and sectioned. *Sargassum muticum* was particularly suitable as the leaves sectioned well and did not contain too much mucilage which otherwise masked the sections. It was important to ensure, both for epilithic and epiphytic crusts, that the crust was on the same side of the host as the knife in order to prevent dragging.

Preparations made from dried material were sectioned in the same way after the material had been thoroughly soaked in water with a little detergent.

Freezing microtome preparations were also used for investigating anatomical structure; they were particularly useful in elucidating ostiolar characteristics since they gave a three dimensional view of the structures concerned. Floridean starch grains showed up well in glycerine jelly/crystal violet preparations but nuclei only occasionally stained.

Further sections were made by standard paraffin wax techniques on material dehydrated through an ethanol/xylene series. The sections were cut at 6–7 μm and stained variously with Masson's trichrome, phosphotungstic acid haematoxylin, Erlich's haematoxylin, or safranin and light green (D. A. Johansen, 1940; Drury and Wallington, 1967): of these Masson's trichrome proved to be the most useful general purpose stain. By using a variety of stains it was possible to emphasise various features such as nuclei and spermatangia.

Herbarium material of the type species of *Pneophyllum fragile, P. rosanoffii, P. confervicolum,* and *Melobesia rosea* was sectioned in Spurr's resin after staining in potassium permanganate (see Woelkerling, 1978 and 1980).

Specimens were examined on a Wild M40 microscope, drawings were made using a drawing tube, and slides were photographed with a Wild photoautomat.

Scanning electron microscopy

Most of the material examined under the S.E.M. was dried by pressing in the usual way for herbarium specimens and the surface of the material then lightly brushed before being mounted.

It was found that air drying was particularly suitable for showing surface features, such as crust cells and epithallial concavities, since this removed surface mucilage, with adherent débris, which otherwise obscured crust details. Features, such as ostiolar filaments, however, were seen more clearly in critical point dried material: for this purpose specimens were fixed in 4% neutralised formalin sea-water, dehydrated in a standard alcohol/acetone series, and dried in a Polaron critical point dryer.

All specimens were mounted on stubs using double-sided 3M Scotch tape and coated with gold/palladium in a Polaron E5000 sputter coater at 1·2 kV for 2–6 minutes. Specimens were examined in a Jeol T20 scanning electron microscope at 20 kV. Images were recorded, using a 60 second scan, on to Ilford FP 4 120 film developed in ID 11 for 6·5 minutes at 20°C.

Sequential field observations

The fresh material upon which the present study has been principally based was collected at regular intervals from various localities on the south coast of England, particularly Bembridge, Kimmeridge, and Beer (Fig. 18). Detailed information will be published elsewhere but most of the material upon which the observations were based is retained as dried herbarium specimens and/or formaldehyde preserved specimens in the possession of the author. A representative selection, including type specimens, is in the British Museum (Natural History).

Laboratory culture

Two series of observations were made on cultured crusts:

(1) Spore germination and segmentation were studied on material obtained *either* by placing crust fragments with fertile conceptacles upside down on microscope slides in Petri dishes containing von Stosch culture medium (Ott, 1966) and placing the Petri dishes in a culture room at 10°C, 8–$\overline{16}$ daylength, 250 lux, *or* by placing a culture slide bearing a single crust type together with clean microscope slides in a vessel of running seawater and allowing settlement of the spores on the slides.

(2) Life history and morphological observations were made on slides bearing crusts initiated in either of the ways mentioned above, the crusts were then located on the slides using an England Finder slide with co-ordinates and the slides placed at an angle in running sea-water in sloping enamel dishes (300 × 250 mm) on a laboratory bench. An air bubbler was placed in each dish. The temperature of the sea-water varied with the season from 2°C to 22°C; natural daylength also varied with the season and in winter it was extended by fluorescent light when the laboratory was in use. Light intensity values up to 700 lux were recorded.

Culture methods were used to separate out a mixture of epilithic *Pneophyllum* spp. growing in close proximity to each other on a piece of glass. The glass was placed in an enamel dish containing twenty-four 75 mm × 25 mm glass slides and sea-water was run through the dish. After about two weeks the glass fragment was removed and the sporelings which had developed on all the slides allowed to grow on in the running sea-water. These crusts were used for clarifying the taxonomy of epilithic *Pneophyllum* spp. as indicated on page 336.

The history of the Corallinaceae

The corallines in general

The history of the classification of the Corallinaceae has been documented by a number of authors in recent years (e.g. Mason, 1953; Littler, 1972; Adey & Macintyre, 1973; Gittins, 1975; Johansen, 1981) either in respect of the Corallinaceae in general or the crustose forms in particular; the problems concerned with the taxonomy and nomenclature of *Fosliella* and *Pneophyllum* have, however, not previously been satisfactorily resolved.

The published history of the coralline algae goes as far back as a mention of *Corallina* by Pliny in the first century A.D. according to Gray (1821). By the end of the sixteenth century the corallines were beginning to be recognised as a group and in general terms their history from that time falls into three periods.

In the first period, until the 1750s, articulated and crustose corallines were usually classed as plants because they were sedentary, although crustose forms were sometimes thought to be inorganic. At this stage, corallines were classified together with several animal groups such as sponges, bryozoans, and corals (including hydroids). Various other calcified algae, such as the red alga *Galaxaura* and the green algae *Halimeda* and *Udotea*, were classified with articulated corallines at this period.

During the next 90 years, all the algae and animals mentioned above were considered by most workers, most notably by Ellis (1755, 1768) and Linnaeus (1758), to be animals; finally in 1837 their plant structure was firmly established by Philippi and the modern period in their history had begun.

The simple crustose Corallinaceae

Introduction

Although the taxonomic section of this study is concerned only with *Fosliella* and *Pneophyllum* of the subfamily Mastophoroideae, the concept of these genera has become confused with other genera of simple crustose corallines, particularly *Dermatolithon* Foslie of the Lithophylloideae and *Melobesia* Lamouroux of the Lithothamnioideae. Since the application of these names undergoes many changes, the principal usages are summarised in Table 1.

Many misconceptions regarding the classification of simple crusts have arisen because authors have not examined type material but have instead based their assumptions on previously mistaken identifications (cf. Dixon, 1970). The following conclusions are based on examination of type material except (notably Esper and Harvey) where this is not available. One of the difficulties encountered in studying type and other published material of simple crusts is that frequently not only are three reproductive types present (tetrasporangial, carposporangial, and bisporangial), but that these often grow intermingled with other simple crustose species. It is necessary, therefore, to obtain a clear view of the author's concept of all the species he recognised in order to distinguish the particular plant he was considering when mixtures were present. An example is Kützing's *Pneophyllum fragile* which was growing on *Sphaerococcus*, together with *Fosliella farinosa* and *Dermatolithon* sp.

E. J. C. Esper

In 1806 Esper published drawings of an epiphytic, crustose coralline growing on *Calliblepharis ciliata* (Huds.) Kütz. No formal description was given but the illustration with diagnosis is eligible for consideration as a valid publication. Esper referred his alga to the animal kingdom and placed it in the genus *Corallina* as *C. membranacea*. Kylin (1956: 202) considered the illustrations to be of the genus *Dermatolithon*. It is true that Esper's Table XII, Figure 1 giving a general view of host and epiphyte, indicates that the epiphyte had the substantial thallus and relatively large, prominent conceptacles, typical of *Dermatolithon*. However, the magnified drawings of his Figures 2, 3, and 4 show the plant to be the species now known as *Melobesia membranacea* (Esper) Lamouroux. The figures show dark-centred conceptacles which are very characteristic of *M. membranacea*; in addition there appear to be several pores in the roof of one conceptacle indicating that this must be a lithothamnioid alga. The wrinkled appearance of the crust in Figure 2 indicates that the plant had a thin thallus which adhered to, and contracted with, the host as it dried. This is typical of *M. membranacea*, but not of *Dermatolithon* the thicker crusts of which normally crack or become detached as the host contracts beneath them. In the final edition of Esper (1830), written by Hammer, the corallines were recognised as plants and *Corallina membranacea* was described.

As discussed under Lamouroux the specific name *membranacea* was taken up by Lamouroux (1812) and transferred to his new genus *Melobesia*. One of the two specimens of *M. membranacea* in Lamouroux's herbarium (CN) is also on *Calliblepharis ciliata* and strongly resembles Esper's drawings. Esper gathered specimens of plants and animals from many scientists, he then drew them and published the illustrations very rapidly, often without the donor's permission

(Silva, 1953). It seems possible, therefore, that the material for Esper's drawing was received from Lamouroux. The specimen now in the Lamouroux herbarium, which has clearly been cut from a larger plant, may even be part of the same material. Unfortunately Esper's material cannot be located. Since Lamouroux did not illustrate this species himself (unlike the other species he described) this would suggest that he considered the drawings made by Esper to be adequate for the purpose.

J. V. F. Lamouroux

The first epithets other than Esper's *membranacea* to be applied to simple crustose corallines were published in 1812 by Lamouroux. He described a new genus, *Melobesia,* with three species: *M. membranacea* based on Esper's *Corallina membranacea, M. orbiculata,* and *M. verrucata*. The species were not described, but the genus was published with the following description:

> 29. MELOBESIA, *Lamx.* Corallinæ sp. Esp. P. entièremement crétacé, naissant en plaques minces sur les plantes marines; cellules formant de petits mammelons. *Corallina membranacea*, Esper. *Melobesiæ verrucata* et *orbiculata*, Lamx. inéd.

In 1816 Lamouroux revised the above generic description and extended it. He also discussed the suprageneric classification of *Melobesia.* He classified the organisms to which the names were applied as 'polypiers' and included them in his 6th Order 'Corallinées'. Lamouroux's 'order' included various non-coralline algae, in addition to crustose and articulated corallines. He said that he had been uncertain as to where the genus should be placed, but because it was chalky he had placed it in the Corallinées. This placement was further justified by the fact that the substance of the organisms was very similar to that of *Amphiroa* and *Corallina* from which they differed only in lacking an axial construction. In this later publication he described four species: *M. membranacea, M. pustulata, M. farinosa,* and *M. verrucata*. The last two were illustrated and there are specimens of all four in Lamouroux's herbarium. The name *M. orbiculata* (Lamouroux, 1812) never appeared again and as no formal description exists, it must remain a *nomen nudum*. No specimen was found under this epithet in the herbarium.

The type species of *Melobesia* Lamouroux must be *M. membranacea* (Esper) Lamouroux (Howe, 1920). Both Lamouroux's material and his description show that some of its conceptacles had roofs with numerous pores which prove it to be a lithothamnioid genus. Of the other species described by Lamouroux, *M. farinosa* now belongs in the genus *Fosliella,* and *M. pustulata* and *M. verrucata* are now regarded as species of *Dermatolithon*.

F. T. Kützing

Kützing's publications were critical in the development of classification of the simple crustose corallines. In his first publication on the subject Kützing (1841) revised Lamouroux's 'Polypieres calcifères' which comprised a mixture of animals, coralline algae and other calcified green and red algae. Apart from *Alcyonidium,* Kützing included only the plants in his revision and he moved *Melobesia* Lamouroux from the Corallinées to 'Die Nulliporen' which was Lamarck's name for the crustose coralline group. The only species of *Melobesia* which Kützing included was *M. membranacea*; his description was clearly of a plant which would now be referred to *Dermatolithon* and he mainly used the name *Melobesia* in that sense thereafter.

By 1843, Kützing had completely revised his classification. He had separated all the non-coralline calcified algae from the corallines and divided the latter into two families: Spongitae containing crustose genera; Corallinae containing articulated genera. Four genera were included in Spongitae: *Hapalidium, Pneophyllum, Melobesia* Lamouroux, and *Spongites*.

Spongites encompassed Philippi's genera of complex crustose corallines *Lithothamnium* and *Lithophyllum*. The other three genera were simple crustose corallines which, literally translated, were described as follows:

Hapalidium – Plants small, leafy-membranaceous, encrusting, pink, stony, attached below, composed of one layer of excentrically radiating cells. Fruit bodies unknown.

Table 1 To show synonymy of genera now recognised as *Pneophyllum, Fosliella, Melobesia,* and *Dermatolithon*.

GENUS NOW recognised	Lamouroux 1812 1816	Kützing 1843–1869	Areschoug in J. G. Agardh 1852	Crouan frat. 1859 1867	Reinsch 1874(?75)	Harvey 1848 1851	Heydrich 1897*b*	Foslie		Howe 1920
								genus	subgenus	
Pneophyllum Kützing		*Pneophyllum* *Phyllactidium* *Hapalidium*	*Hapalidium*	*Hapalidium* *Melobesia*	?*Plectoderma*	?*Lithocystis* *Melobesia*	*Melobesia*	*Melobesia*	*Eumelobesia* (1898*b*, 1900*b*)	*Fosliella*
								Dermatolithon (1898*b*)		
								Melobesia	*Heteroderma* (1898*b*, 1900*b*, 1905*b*)	
								Lithophyllum	*Carpolithon* (1905*b*)	
								Melobesia	*Pliostroma* (1908*b*, 1909)	
								Heteroderma	*Euheteroderma* (1909)	
Fosliella Howe	*Melobesia*	*Melobesia*	*Melobesia*	*Melobesia*			*Melobesia*	*Melobesia*	*Eumelobesia* (1898*b*, 1900*b*, 1905*a*)	*Fosliella*
Melobesia Lamouroux	*Melobesia*	*Hapalidium*	*Melobesia*	*Hapalidium* *Melobesia*	?*Plectoderma*	?*Lithocystis*	*Melobesia* *Epilithon*	*Lithothamnion*	*Eulithothamnion* (1898*a*)	
								Lithothamnion	*Epilithon* (1898*b*, 1900*b*)	
								Lithophyllum	*Carpolithon* (1905*b*)	
								Epilithon (1909)		
Dermatolithon Foslie	*Melobesia*	*Melobesia*	*Melobesia*	*Melobesia*		*Melobesia*	*Melobesia*	*Melobesia* (1898*a*)		
								Melobesia	*Heteroderma* (1898*b*, 1900*b*)	
								Dermatolithon (1898*b*, 1900*b*, 1909)		
								Lithophyllum	*Carpolithon* (1900*b*)	
								Lithophyllum	*Lepidomorphum* (1900*b*)	
								Lithophyllum	*Dermatolithon* (1905*a*)	

Pneophyllum	– Plants small, extended-leafy, encrusting, stony, pale, of more than one cell layer, the lower cells rounded and loosely coalescent, the upper cortical cells minute, rounded, all entirely unorganised. Fruit bodies unknown.
Melobesia	– Plants small, extended-leafy, encrusting, adherent, stony, composed of layers of cells stratified both vertically and horizontally, the lower cells vertically elongated, upper (cortical) cells very short, surface cells radially arranged. Cystocarps immersed, papilliform, spermatus i.e. sporangia oblong, red, farctate (without a stalk).

In addition Kützing described a genus of green alga, *Phyllactidium*, which included the simple crustose coralline *P. confervicola*. This he later (Kützing, 1849) reclassified as *Hapalidium phyllactidium*.

As mentioned previously, Kützing's *Melobesia* species mainly belong to the genus *Dermatolithon* (Lithophylloideae). An important exception is *Melobesia farinosa* which, on the basis of an examination of Kützing's herbarium specimens, belongs to *Fosliella*.

In 1843, Kützing described only one species of *Hapalidium* – *H. roseolum* 'Auf Bryopsis Balbisiana in Golf von Spalato! – März 1835' (Fig. 55B). The type specimen is L. no. 941.149.413. Despite the implications of Kützing's generic description, conceptacles and epithallial cells are both present. Some of the conceptacles are tetrasporangial and have numerous pores in the roof thus establishing the specimen as a species of the Lithothamnioideae. Personal investigation indicates that it is in fact referable to *Melobesia membranacea*. Isotypes are widely distributed and have been seen, for example, in Le Jolis's herbarium (CHE). Thus, the type species of the genus *Hapalidium* was based on a specimen of the previously described type species of *Melobesia* Lamouroux. *Hapalidium* is therefore a synonym of *Melobesia*.

Pneophyllum remained a monospecific genus throughout Kützing's publications. The single species, *P. fragile* (Type: L. no. 941.241.152), was described (Kützing, 1843) as '*P. cinereo-albidum,* irregulariter incrustans, fragile. An *Rhyncococcus coronopifolius* im Mittelmeere'. In 1845 Kützing extended its distribution to the Dalmatian coast, and added 'other algae' to the original host. The type specimen of *P. fragile* (Fig. 24) bears three distinct taxa which would now be recognised as:

1. *Fosliella farinosa.*
2. A few scraps of *Dermatolithon* sp.
3. *Pneophyllum fragile.*

Because the generic name has not been used other than by Kützing and is being resurrected in the present publication and extended, it is of particular importance to establish the reasons for attaching the name to the taxon in question and not to *Fosliella farinosa* or *Dermatolithon* sp. The arguments are as follows:

(*a*) Had Kützing been referring to the *Dermatolithon* he would presumably have named it *Melobesia* for the reasons already given.

(*b*) Although Kützing did not list *Melobesia farinosa* in 1843, he included it in his 1845, 1849, and 1869 publications. His view of it gradually changed (confirmed by examination of herbarium specimens) but generally it was a species with prominent conceptacles as distinct from the flat conceptacles of *Pneophyllum*.

(*c*) Another specimen of *Sphaerococcus* (= *Rhyncococcus*) (L. no. 943.68.280) looking very similar to the type material of *Pneophyllum fragile,* but bearing only *Fosliella farinosa* and *Dermatolithon pustulatum,* was left unidentified. Had Kützing been applying the epithet *Pneophyllum fragile* to either of the other taxa he would presumably have labelled the specimen as such.

(*d*) The illustration in *Tabulae Phycologicae* (Kützing, 1869) shows a thin crust composed of rectangular cells with contents among which Kützing had observed some empty looking cells in intercalary positions. It is probable that these are what would now be recognised as intercalary trichocytes which could not therefore belong to *Fosliella farinosa*.

Since Kützing's publications, species of *Pneophyllum* have been referred to many genera, including *Melobesia* Lamouroux, *Hapalidium* Kütz., *Lithocystis* Harvey, *Plectoderma* Reinsch, *Heteroderma* Foslie, *Guerinea* Picquenard, and *Fosliella* M. Howe (Tab. 1). A description of the type species of *Pneophyllum, P. fragile*, is given on page 356.

W. H. Harvey

Harvey (1841) did not include coralline algae in the first edition of his *Manual of the British Marine Algae* as at that time he considered them to be animals. In the second edition Harvey (1849) included the 'Order IX Corallinaceae' of which 'suborder II Nulliporae' contained all the complex and simple crustose species under the name *Melobesia* and also the non-calcareous genus *Hildenbrandia*. 'Suborder III Lithocysteae', the thallus of which Harvey described as being hyaline as opposed to the thallus in the Nulliporae which was opaque, contained the single taxon *Lithocystis allmanni* which had been published previously (Harvey, 1848).* Allman himself described the species which consisted of minute, sterile, calcareous crusts growing on *Lomentaria clavellosa,* which was in turn attached to an oyster he was eating while dining with Harvey. Since that time, *Lithocystis allmanni* has haunted the synonymy of the simple crustose corallines, appearing as a synonym of many different species, usually with a question-mark. It has proved quite impossible to find the type specimen despite patient and painstaking searches by the curators of herbaria at Trinity College Dublin, St. Andrews, Edinburgh, and the British Museum (Natural History), and it seems unlikely that a definite identification will ever be made of this species.

On the basis of the present investigation it was probably not *Melobesia membranacea* (with which it has most often been synonymised) since the cells appeared less elongated than is usual in this species. It was probably, therefore, a species of *Pneophyllum* or *Fosliella* since no other genera form thin, epiphytic, calcareous crusts of this sort. If the plant was *Melobesia* or *Pneophyllum, Lithocystis* would be a later synonym of these genera. If it was *Fosliella,* the name *Lithocystis* would have priority, but unless the specimen can be found further identification is not possible.

P.-L. and H.-M. Crouan

The Crouan brothers worked as pharmicists at the naval base at Brest in the mid-nineteenth century. They were interested in all aspects of botany and made extensive collections of plants, particularly algae, lichens, and mosses, in the locality. They also made dredge collections of algae in the Rade de Brest area over a number of years. They distributed an exsiccata of algae from Finistère (P.-L. and H.-M. Crouan, 1852). The history of their collections was documented by Dixon (1967) who explained their participation in the production of Lloyd's exsiccata (1847 onwards) and the way in which their own collections came to be housed at the Laboratoire de Biologie Marine, Concarneau under far from ideal conditions. Dixon (1967) commented that the 'wrappers and boxes in which the Crouan collection is stored . . . will soon be of more interest to the mycologist than the phycologist'.

Since Dixon's visit to Concarneau in 1964, the laboratory has been rebuilt and the collections are now housed under clean, dry conditions in the library. When the collections were first acquired by Concarneau they were curated by a local, amateur botanist, Dr C.-A. Picquenard, who published a catalogue of the Florideae (Picquenard, 1912*b*).

While the collections at Concarneau have a particular claim to suitability when selecting type specimens because they represent the Crouans' working collection, specimens were also distributed by the Crouans to other herbaria. The Thuret/Bornet collection in Paris, for example, contains many specimens distributed prior to the publication of *Florule du Finistère* (P. & H. Crouan, 1867).

In the present context the work of the Crouan brothers is of particular importance because they published (P. Crouan & H. Crouan, 1859) a paper describing epilithic, simple crustose corallines in the genus *Hapalidium* Kützing. This publication seems to have been inspired by the collections made when dredging in the Rade de Brest on 12 December 1858 and the Rade de

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* details of the dating of the *Phycologia Britannica* fascicles are to be published by Price.

Camaret on 4 and 17 December 1858 and 24 and 28 January 1859, while data obtained on earlier visits were also used. Of the four *Hapalidium* species discussed in the 1859 paper, three were new (*H. zonale* now *Pneophyllum zonale, H. coccineum* now *Melobesia membranacea, H. callithamnioides* now *Pneophyllum confervicolum* f. *minutulum*). A further new species in the closely related genus *Melobesia, M. myriocarpum* now *Pneophyllum myriocarpum*, was listed as a *nomen nudum* a year later (P. Crouan & H. Crouan, 1860) and a description published in the 'Florule' (P. Crouan & H. Crouan, 1867).

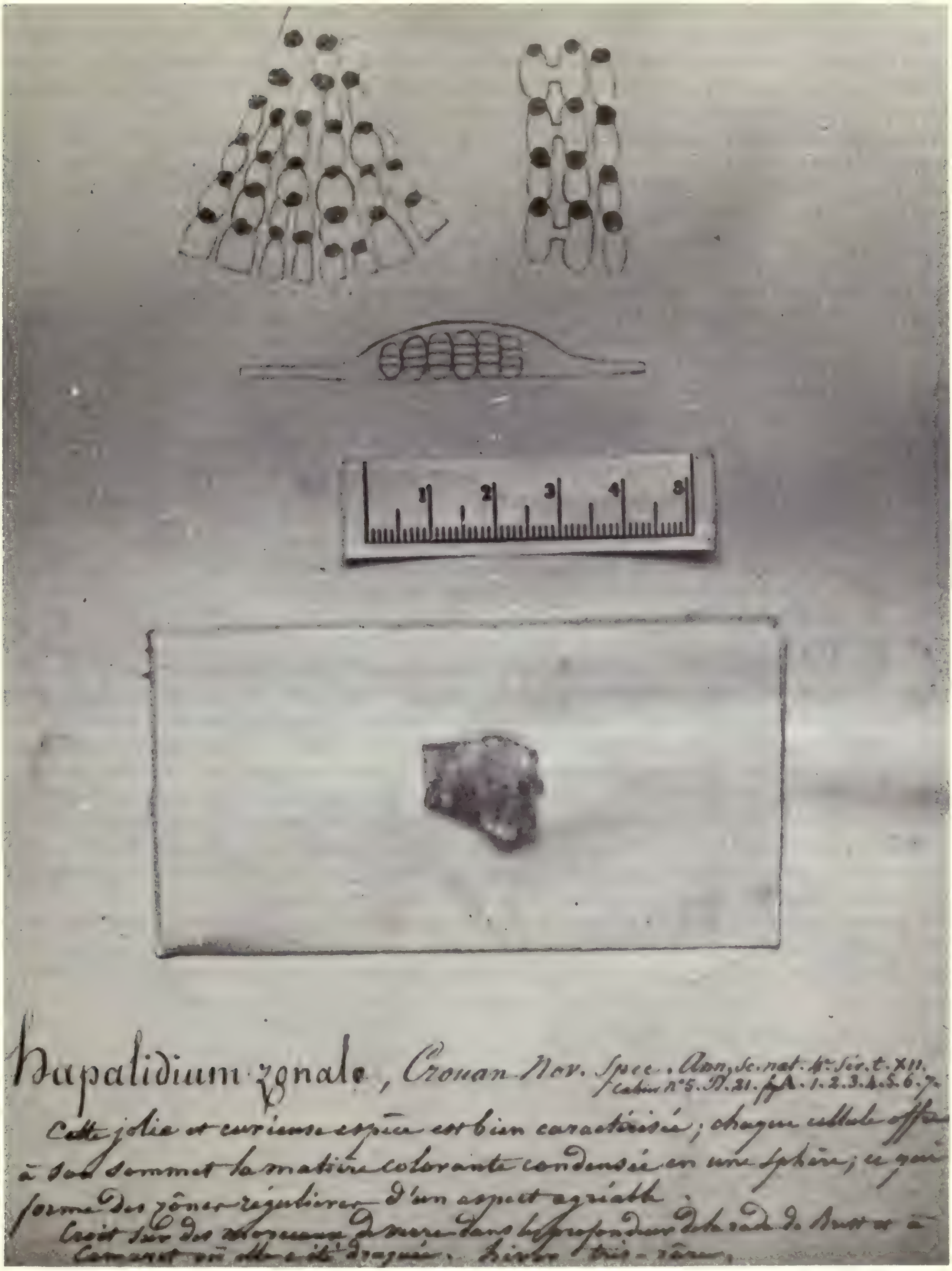
Since the Crouans' publications the systematics of these species has become particularly confused, both because of the technical difficulty of examining them adequately, and because the location of the Crouan collections was unknown. Crouan specimens of these species are present in Paris but they are for the most part either undated or bear a collection date later than the publications. On a visit to Concarneau in June 1979 it was found that all the specimens relevant to the present publication were in the collection, clearly labelled by the Crouan brothers with identification, locality, and date (e.g. Figs 61A, B; 78A, B, D). The specimens were in packets which had been mounted on herbarium sheets by Picquenard and the sheets were in folders labelled according to the catalogue (Picquenard, 1912*b*). The synonymy was presumably based on the works of Foslie (1900*a*, 1908*a, b*) who had reviewed the Crouan species on the basis of the Crouans' descriptions and drawings (P. Crouan & H. Crouan, 1859, 1867) and Crouan specimens obtained from Paris. In addition to the packeted material, several species (e.g. *Hapalidium zonale*) are represented by a specimen carefully mounted on an herbarium sheet with a copy of the published description and illustration (Fig. 1). Hippolyte-Marie was the artist of the two brothers and he probably mounted the specimens in this way. These sheets seem to have been intended as representative of the species concerned, but since the specimens are, for the most part, undated and unlocalised, the material in packets bearing the necessary data were preferred as types (see *Pneophyllum myriocarpum, P. zonale*).

S. M. Rosanoff

Rosanoff was a Russian phycologist who went to Cherbourg to work on crustose coralline algae under Le Jolis; he completed his thesis there and it was published in 1866. Rosanoff then returned to Russia where he became Director and Chief Botanist of the Botanical Garden, St. Petersburg. He embarked on a packet boat in late 1870, at Napoli, heading for Palermo, where he intended to remain until May 1871 recovering from haemoptysis and studying the physiology of algae at the same time. Unfortunately he did not reach Palermo since he died from an accidental fall on board ship on 3 December 1870. He was reported to have been very weak and to have been advised by friends in Napoli not to attempt the journey (P. C. Silva, *in litt.*).

Rosanoff's (1866) publication is of particular importance in the present context since he gave excellent descriptions and illustrations of a number of epiphytic simple crustose Corallinaceae in conjunction with an analysis of their structure and morphogenesis which forms the foundation for subsequent investigations of these algae. It seems that, until the present investigation, the original material upon which Rosanoff based his work has not been re-examined; Le Jolis's material, commented on by Foslie (1900*a*), came from Le Jolis's distributed exsiccatae.

It is clear from Rosanoff's (1866) text that he worked with living as well as herbarium material, but in his species descriptions he cites only herbarium material collected by Le Jolis, Lloyd, Lenormand, Areschoug, and other phycologists. The herbarium of Le Jolis (1823–1904) is housed in the Société des Sciences Naturelles et Mathèmatiques de Cherbourg. The algae are, for the most part, contained in strapped bundles; they are in excellent condition and appear to have remained undisturbed since they were arranged by Le Jolis. Until 1979 the herbarium was in the nearby Museum and seems to have been somewhat inaccessible, but the specimens are now stored accessibly and under suitable conditions. I examined the material of simple crustose corallines in June 1980 and found that, with very few exceptions, they were arranged according to Rosanoff (1866) with most of the specimens having their name written in Rosanoff's hand (Fig. 33), while others had been labelled or relabelled by Le Jolis (Fig. 33). In addition there is a bound set of Le Jolis's exsiccata *Algues marines de Cherbourg,* some specimens of which



Hapalidium zonale, Crouan Nov. Spec. Ann. Sc. nat. 4e Sér. t. XII. Cahier n° 5. Pl. 21. fig. A. 1. 2. 3. 4. 5. 6. 7.

Cette jolie et curieuse espèce est bien caractérisée; chaque cellule offre à son sommet la matière colorante condensée en une sphère; ce qui forme des zônes régulières d'un aspect agréable.
Croît sur des morceaux de maerl dans les profondeurs de la rade de Brest et à Camaret où elle a été draguée. Hiver très-rare.

Fig. 1 Specimen of *Hapalidium zonale* mounted by the Crouan brothers (CO).

duplicate those in the bundles. Finally there is a bound volume of Le Jolis's specimens made by Corbière who worked under, and finally succeeded, Le Jolis as Director of the Society. These appear to have been extracted from the bundles of specimens and are thus probably equally suitable for the selection of type material. In the present study, however, types were selected from the specimens in the bundles.

No notes, manuscript, or specimens collected by Rosanoff himself have been traced either at Cherbourg or St Petersburg; Rosanoff, however, visited the herbarium at Caen (see Johnson & Hensman, 1899: 26), where he examined Lamouroux's specimens and also those of Lenormand and other phycologists. On a visit to Caen in June 1980 I found that Rosanoff had annotated the collections there on two separate occasions as there were notes in two slightly different styles of writing (Fig. 19); in the absence of any other annotations or manuscript these notes are, therefore, of particular importance in interpreting Rosanoff's work.

In order to clarify the taxonomy of British species of *Pneophyllum* and *Fosliella,* it is essential to understand Rosanoff's publication, not only because he made the first detailed investigations on these genera but also because the material he described mostly came from the Cherbourg area and is similar to that found in England and Ireland. In addition to being able to locate, in Herb. Le Jolis, virtually all the samples cited by Rosanoff, identification of his taxa is made feasible by the fact that he made excellent illustrations, the relevant plates of which are reproduced here (Figs 2–6) together with those captions of Rosanoff's that are relevant to the present study.

As Rosanoff (1866: 6) says, in the introduction to his work the identification of corallines 'is made difficult by lack of outstanding characters . . . they are very polymorphic . . . their features are often much influenced by the substratum . . . it is therefore necessary to penetrate details of structure and reproduction to find constant characters not influenced by external circumstances' [translation].

Rosanoff gives detailed descriptions and illustrations of the way in which a simple crust grows (Figs 2 [1, 2, 5, 7]*), based mainly on *Pneophyllum rosanoffii* (as *Melobesia lejolisii*). Unfortunately he makes a wrong interpretation of the reproductive bodies (Rosanoff, 1866: 39). He regards asexual conceptacles as having multiperforate roofs and bearing the true 'tetraspores' or 'sphaerospores', while all conceptacles with single pores are sexual cystocarps and bear either 'spores' or antheridia. The 'spores' are 2- or 4-partite (i.e. now recognised as bi- and tetrasporangia) when mature, and globose (i.e. now recognised as carposporangia) when young. It follows from this that only the lithothamnioid species (*Melobesia membranacea* and *M. corticiformis*) of the simple crusts show all reproductive stages – all other species, with only single-pored conceptacles, lack true 'tetrasporangia'. This explains the apparently curious terminology of some of the plate captions.

Rosanoff placed all the simple crusts in the genus *Melobesia* and the species relevant to the present study are as follows: *M. lejolisii, M. membranacea, M. farinosa, M. corticiformis,* and *M. rosea.* These will now be discussed and interpreted with the benefit of subsequent knowledge.

1. *Melobesia lejolisii* Rosanoff (1866: 62)

Rosanoff records this species as growing on *Zostera* and *Bornetia secundiflora*. He describes it as being a thin crust becoming more than two cells high only in the region of the conceptacles, the conceptacles are scarcely raised, about twice as wide as high, and with an ostiole surrounded by long, gelatinous hairs when mature but simple when young. I consider that three distinct entities are included: a) *Pneophyllum lejolisii,* b) *P. rosanoffii,* and c) *P. concollum.*

(*a*) *Pneophyllum lejolisii* (Figs 2 [4, 10, 12]; 6 [9–11])

This is the most common *Pneophyllum* species growing on *Zostera* throughout Europe. It has a vegetative thallus composed of hypothallium and epithallium only, which is rather lightly calcified and has more or less iso-diametric crust cells in surface view. The conceptacles are flattened and the ostiole is simple. This entity was considered by Rosanoff to be a young form of

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* The numbers in square brackets refer to the individual drawings on Rosanoff's plates.

Melobesia lejolisii before the ostiolar filaments had developed. It is illustrated by a surface view of the ostiole (Fig. 2 [12]), surface views of the delicate crust cells (Figs 6 [9–11]), and further surface views of the crust (Figs 2 [4, 10]) which again show the square cells and (Fig. 2 [4]) a typical surface view of a *lejolisii* conceptacle which Rosanoff describes as showing three sporangia (not visible in the present reproduction).

In the citations Rosanoff quotes '*Melobesia membranacea* Aresch. in J. Ag. Spec. II, p. 512 (partim)' and this judgement was presumably based on two specimens which Areschoug sent Rosanoff and which are typical of the present species. One of these, Areschoug no. 2 (Fig. 28), is now designated lectotype and it is to be found in the *Melobesia membranacea* folder in Herb. Le Jolis (CHE).

(*b*) *Pneophyllum rosanoffii* (Figs 2 [1–3, 5–7, 11])

This is the entity considered by Rosanoff to be the mature form of *Melobesia lejolisii* with long, gelatinous hairs round the ostiole. In France this species occurrs commonly on *Zostera*, often together with *P. lejolisii*, but it also occurs widely on *Halopitys incurvus*. Because I first investigated this entity on British material of *Halopitys* (it is not common on *Zostera* in England), I was able to establish its identity in isolation from *Pneophyllum lejolisii*, but it was easy to appreciate, when I later examined *Zostera* specimens from France and Ireland bearing both species, how Rosanoff came to view the two elements as one species. *Pneophyllum rosanoffii* has larger, more rectangular and more calcified cells than *P. lejolisii*, and these are clearly illustrated in Figures 2 [1–3] and [5–7] while the ostiolar filaments are shown in Figure 2 [11]. It is possible that Figures 2 [8] and [9] illustrate a conceptacle of this species, but I have never seen swollen paraphyses in *P. rosanoffii* and in my opinion this conceptacle belongs to *P. concollum* (see below) in which such paraphyses are often present.

Among the citations Rosanoff quotes '*Melobesia farinosa* Kuetz. Spec. alg. p. 696 (sec. specim. a cel. Auct. determ.); Le Jol. Liste des alg. mar. de Cherb. p. 150! – non Lamx.'. This refers to a Le Jolis collection (no. 1200) from Querqueville, Cherbourg, 31 December 1857 (Fig. 33) which was subsequently distributed in a Le Jolis exsiccata as no. 283. The collection comprised many *Zostera* leaves all covered with deep pink crusts of *Pneophyllum rosanoffii*, unmixed with any other species. Le Jolis sent some leaves to Kützing (now in L. no. 941. 150. 75) who identified the epiphyte as *Melobesia farinosa* under which name Le Jolis (1863) included it in his list of algae from Cherbourg. Kützing (1869) subsequently based his illustration of *M. farinosa* in Tabulae Phycologicae on this specimen.

Several duplicates of this material are present in the *Melobesia lejolisii* folder in Herb. Le Jolis (CHE) and there is no doubt that this is the material on which Rosanoff principally based his description of the mature state of *Melobesia lejolisii*. I have described *Pneophyllum rosanoffii* (Fig. 33) from among these specimens partly because it is historically suitable but also because it is a pure stand of the species.

Two other specimens are present in the *Melobesia lejolisii* folder in Herb. Le Jolis; these were collected by Le Jolis, Cherbourg, 1844 and Thuret, Anse Ste. Anne, 25 January 1853. Both would have been examined by Rosanoff and both are *Pneophyllum rosanoffii*.

(*c*) *Pneophyllum concollum* (Figs 2 [8–9]; 3 [1–2])

When listing the hosts on which *Melobesia lejolisii* grew, Rosanoff included *Zostera* and *Bornetia secundiflora*. There are no samples of *Bornetia* in the *lejolisii* folders now, but there are many samples collected by Le Jolis in the Cherbourg area on 26 February 1857 and 18 February 1859 in both the *Melobesia rosea* and *M. membranacea* folders. The crusts on *Bornetia* bear flat conceptacles and are of *Pneophyllum concollum*. In my opinion Rosanoff originally thought these to be *Melobesia lejolisii,* but subsequently changed his mind and removed them to either *M. rosea* or *M. membranacea*. This entity is discussed further under *Pneophyllum concollum* (*q.v.*). Almost certainly the conceptacle illustration with balloon-like paraphyses (Figs 2 [8–9]) belongs to *Pneophyllum concollum*, which is a further indication that it was on this material that Rosanoff based his record of *Melobesia lejolisii* growing on *Bornetia*.

2. *Melobesia membranacea* Lamouroux (Rosanoff, 1866: 66) (Figs 3 [6–9], [13–16]; 4 [1])

The description, illustration, and most of the herbarium material of this taxa conforms to the concept of *M. membranacea* (Esper) Lamouroux as currently accepted. It is significant that *Bornetia secundiflora* is not listed as one of the hosts on which *M. membranacea* grows, despite the fact that a specimen of *Bornetia* bearing *Pneophyllum concollum* is present in the *M. membranacea* folder. This is a further indication that Rosanoff changed his mind about the crusts he had originally thought to be *M. lejolisii* on *Bornetia*, and subsequently reidentified them.

3. *Melobesia farinosa* Lamouroux (Rosanoff, 1866: 69) (Figs 3 [3, 5, 10–12]; 4 [2–13]; 5 [1, 10]; 6 [12])

The description, illustration, and majority of specimens agree well with the present concept of *Fosliella farinosa*. Rosanoff gives the first description of the terminal trichocytes in this species, calling them heterocysts because he thought they were probably analogous with the heterocysts of blue-green algae.

Included among the specimens, however, are hosts bearing mixtures of epiphytic crusts such as a specimen labelled (in print) 'no. 240 Herb. A. Le Jolis *Melobesia pustulata* Lamx. (sur le *Rhodymenia palmata*) 30 novbre 1859, Cherbourg' and further annotated '*Melobesia farinosa* Lamx. Rosanoff' in Le Jolis's hand. I have seen further specimens of this collection in CN and PC and all show the mixture of *Fosliella farinosa* and *Pneophyllum limitatum* typical also of autumn-gathered *Palmaria palmata* in southern England. One or two other specimens identified by Rosanoff as *Melobesia farinosa* also bear *Pneophyllum limitatum*, and it is evident that Rosanoff did not distinguish between the two species.

4. *Melobesia corticiformis* Kütz. (Rosanoff 1866: 76) (Figs 2 [14–16])

This is synonymous with *Melobesia membranacea* (Esper) Lamouroux as currently accepted.

5. *Melobesia rosea* Rosanoff (1866: 77) (Figs 3 [1, 2])

Rosanoff introduces this species by saying that, although he has frequently mentioned *M. rosea* in the course of his work (he used it as an example in his introductory discourse on structure and compared several other species with it), he is not entirely convinced that it is a good species.

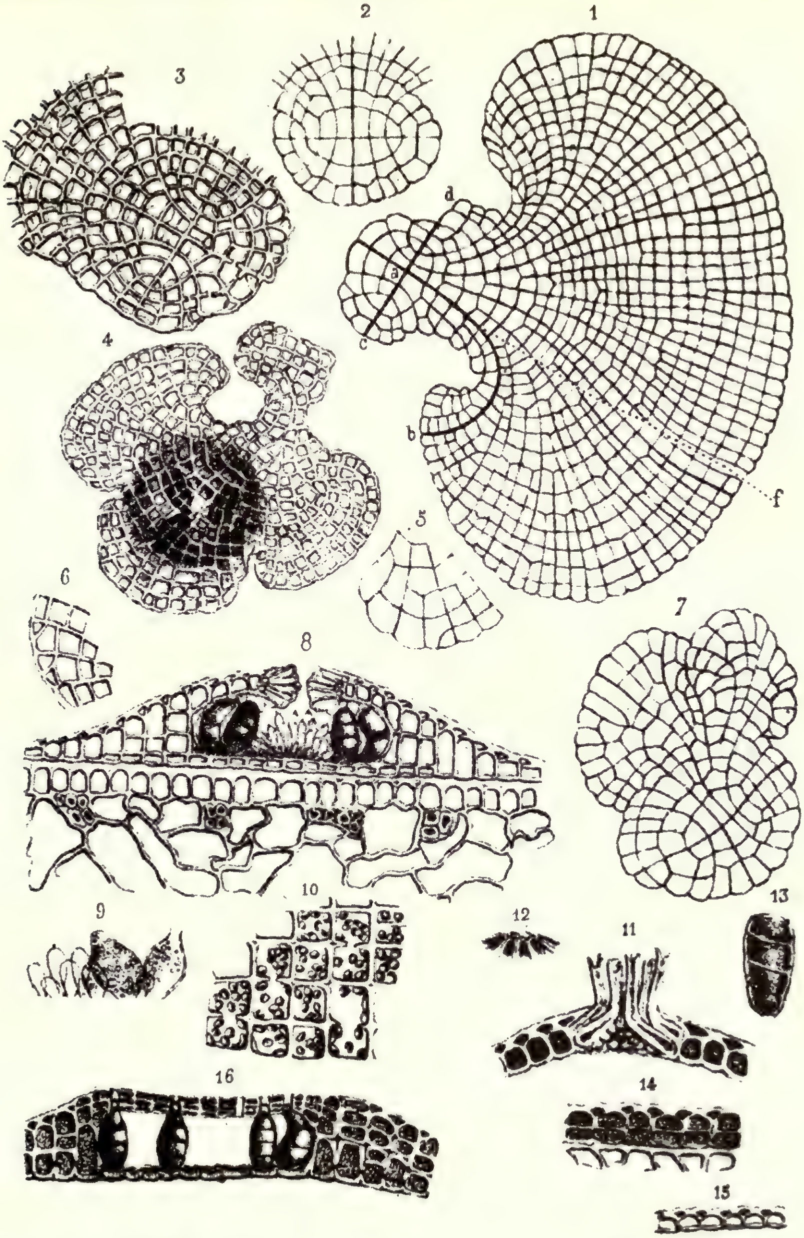
Rosanoff identified certain crusts growing on *Bornetia secundiflora* as '*Hapalidium roseum* Kuetz.' (an error or intentional change of name introduced by Areschoug (1852: 509) for *H. roseolum* Kützing (1843: 385)). *Hapalidium roseolum* grew on *Bryopsis balbisiana* in the Adriatic, the holotype is in Leiden (no. 941.149.413), and an isotype, sent to Rosanoff by Kützing, is in the *Melobesia rosea* folder in CHE (Fig. 55B). Rosanoff made the combination

Fig. 2 From Rosanoff (1866): *Recherches anatomiques sur les Mélobésiées.*

PLANCHE I

Fig. 1. – Jeune fronde de *Melobesia Lejolisii*; on voit qu'une partie seulement (environ un quart) de la fronde primitive orbiculaire, s'est développée en une fronde spathuliforme. Les lignes *cd* et *af* montrent l'angle dans lequel, lors d'un accroissement régulier, aurait dû être renfermé tout le tissu qui se trouve maintenant entre *ab* et *ed*. (Grossissement de 350 diamètres). **Fig. 2.** – Partie primitive d'une fronde de *M. Lejolisii*, avec une disposition bien régulière des cloisons. (Gross. de 350 diam.). **Fig. 3.** – Une fronde pareille, dans laquelle l'accroissement concentrique a duré plus longtemps. (Gross. de 350 diam.). **Fig. 4.** – Une jeune fronde de *Melob. Lejolisii* avec un cystocarpe jeune, dont l'ostiole est en voie de formation; la disposition des cellules, qui constituent la voûte, est la même que dans le reste de la fronde. Au travers de la voûte transparente, on voit trois sporanges. (Gross. de 200 diam.). **Fig. 5 et fig. 6.** – Parties marginales d'un ramule, dans lesquelles on voit le commencement de la ramification des séries cellulaires. (Gross. de 600 diam.). **Fig. 7.** – Cette figure montre la confluence assez irrégulière de deux ramifications frondales. (Gross. de 350 diam.). **Fig. 8.** – Coupe verticale d'un cystocarpe du *M. Lejolisii*; la couronne de poils n'est pas encore formée. (Gross. de 350 diam.). **Fig. 9.** – Paraphyses et sporanges de *M. Lejolisii* dans leur état le plus jeune, (Gross. de 600 diam.). **Fig. 10.** – Une partie de la fronde du *M. Lejolisii,* dans laquelle on voit plusieurs copulations de cellules voisines. La préparation n'a pas été traité par un acide. (Gross. de 600 diam.). **Fig. 11.** – La couronne de poils, qui entoure l'ostiole; les poils sont un peu désorganisés à leurs extrémités. (Gross. de 600 diam.). **Fig. 12.** – Un ostiole, dont les poils ne se sont pas encore élevés. (Gross. de 320 diam.). **Fig. 13.** – Un sporange avec des cloisons inclinées. (Gross. de 350 diam.). Dans les fig. 1 à 7 et 10 les cellules corticales ne sont pas indiquées, pour plus de simplicité. **Fig. 14 et 15.** – Coupes verticales et radiales de la fronde du *Melob. corticiformis*; la fig. 14 est plus rapprochée du bord de la fronde, tandis que la fig. 15 est prise dans son milieu. (Gross. de 600 diam.). **Fig. 16.** – Fructification tétrasporique du *Melob. corticiformis*, suivant une coupe verticale qui n'a pas été traitée par un acide. (Gross. de 350 diam.).

Mém. de la Soc. Imp des sc. nat. de Cherb. T. XII. PL. I.



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Ad nat. del. et lith. S. Rosanoff. *Imp. Becquet à Paris.*

10mm

Melobesia rosea based on '*Hapalidium roseum*', but the name should be *M. roseola* (Kütz.) Rosanoff.

The type specimen of *Hapalidium roseolum* is, in fact, material of *Melobesia membranacea*, as are isotypes seen in CHE and various other herbaria. On the other hand, the specimens of *M. rosea*, which are all epiphytic on *Bornetia secundiflora*, in CHE are of a quite separate entity belonging to the genus *Pneophyllum* and of the species herein described as *Pneophyllum concollum*. Only two illustrations (Figs 3 [1, 2]) of *Melobesia rosea* are given, and as these are of small fragments of crust, they are not diagnostic. However, as mentioned under *Melobesia lejolisii*, the illustration of a tetrasporangial conceptacle attributed to that species (Figs 2 [8, 9]) strongly resembles *Pneophyllum concollum* in the ostiole structure and balloon-like paraphyses, which again suggests that Rosanoff's record of *M. lejolisii* on *Bornetia* was in fact *Pneophyllum concollum*.

Because Areschoug changed the epithet of *Hapalidium roseolum* to *roseum*, it would in fact be possible to use the epithet *roseum* for the present taxon, but this would lead to confusion and so the new name, *Pneophyllum concollum*, has been created and a full description of the taxon is given on page 402.

A summary of the names under which the taxa *P. rosanoffii, P. lejolisii,* and *P. concollum* have been published is given in Table 2.

P. F. Reinsch

In 1874 Reinsch described a new genus of epiphytic, simple crustose corallines – *Plectoderma*. Two species were described and illustrated from sterile material, of which *P. minus* was probably *M. membranacea* judging by the cell shape and germination disc pattern. *P. majus* was possibly a species of *Pneophyllum*. No specimens have been found of either species so further identification is not possible.

F. Heydrich

Heydrich was working and publishing at the same time as Foslie. Initially Heydrich (1897*a*) classified all simple crusts as *Melobesia*. However, he quickly appreciated (Heydrich, 1897*b*) that *M. membranacea*, with many-pored tetrasporangial conceptacles, should be separated from the genera with single-pored conceptacles. He took the view that the single-pored genus should be *Melobesia,* typified by *M. farinosa* Lamouroux and therefore erected a new genus, *Epilithon*, for the many-pored species *membranaceum*. This classification was followed most notably by Foslie, Rosenvinge, Lemoine, Kylin, and Suneson.

Fig. 3 From Rosanoff (1866).

PLANCHE II.

Fig. 1. – Coupe verticale et en même temps radiale de la fronde du *Melob. rosea*; on voit les cellules frondales et audessus de celles-ci les cellules corticales. Le substratum est une branche de *Bornetia secundiflora*. (Grossissement de 600 diamètres). **Fig. 2.** – Coupe verticale et en même temps tangentielle de la même plante; ici les cellules corticales apparaissent sous la forme rectangulaire. (Gross. de 350 diam.). **Fig. 3.** – Jeune fronde de *Melob. farinosa,* croissant sur le *Padina pavonia,* vue d'en haut. On distingue la position alternante des hétérocystes et l'on remarquera que l'accroissement concentrique se maintient très longtemps. (Gross. de 200 diam.). **Fig. 4.** – Figure théorique qui montre de quelle manière devraient se succéder les parois tangentielles et radiales, si l'accroissement idéal, qu'on peut déduire de ce qu'on voit se produire dans la nature, pouvait se réaliser rigoureusement. **Fig. 5.** – Une fronde circulaire du *M. farinosa* (sur *Padina pavonia*), couverte de cystocarpes. (Gross. à la loupe.). **Fig. 6.** – L'ostiole et la partie de la voûte environnante, dans le *Melob. membranacea,* vus d'en haut. (Gross. de 600 diam.). **Fig. 7.** – La voûte d'une fructification tétrasporique, vue d'en haut. (Gross. de 600 diam.). **Fig. 8.** – Commencement d'une fronde du *M. membranacea.* (Gross. de 350 diam.). **Fig. 9.** – Une fronde encore orbiculaire de *M. membranacea* (sur *Furcellaria fastigiata*). (Gross. de 350 diam.). **Fig. 10.** – Hétérocyste du *M. farinosa*, vu d'en haut. (Gross. de 640 diam.). **Fig. 11.** – Coupe verticale de la fronde du *Melob. farinosa*; on voit un hétérocyste avec son orifice. (Gross. de 600 diam.). **Fig. 12.** – Coupe pareille, avec deux hétérocystes. (Gross. de 600 diam.). **Fig. 13.** – Coupe verticale et médiane d'un cystocarpe de *Melob. membranacea* (sur *Furcellaria fastigiata*). (Gross. de 350 diam.). **Fig. 14.** – Coupe verticale et médiane d'un conceptacle renfermant les anthéridies du *M. membranacea*; on voit devant l'orifice un certain nombre de spermatozoïdes. (Gross. de 350 diam.). **Fig. 15.** – Ces spermatozoïdes sous un grossissement de 1300 diamètres; les six inférieurs ont été traités par la teinture d'iode et montrent au centre un granule. **Fig. 16.** – Coupe verticale et tangentielle de la fronde du *Melob. membranacea*, dans le voisinage des organes de la fructification; elle consiste en quatre rangées de cellules superposées. (Gross. de 350 diam.).

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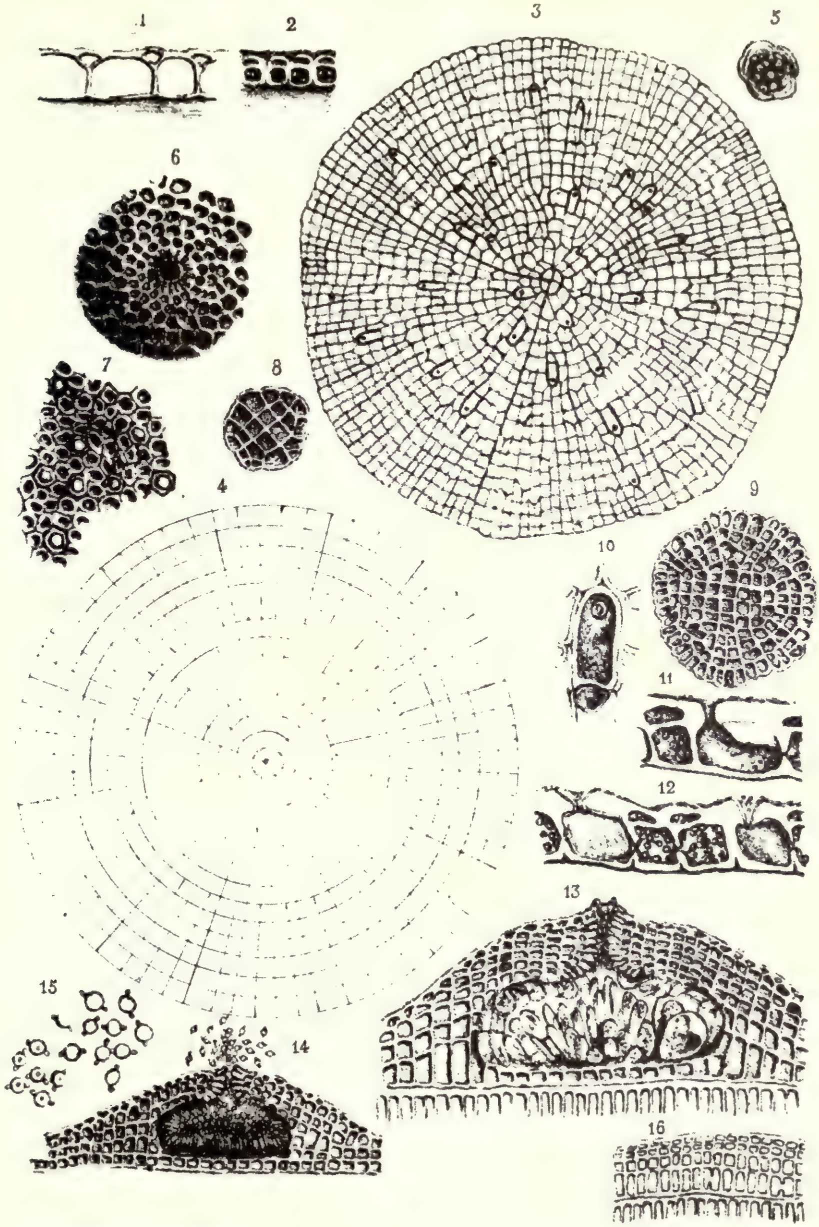
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Ad nat. del. et lith. S. Rosanoff. *Imp. Becquet, à Paris.*

M. H. Foslie

Foslie's works on coralline algae published during his life-time appeared between 1895 and 1909. His last work (Foslie, 1929) was edited by Printz and published posthumously. In this relatively short period Foslie's views on the classification of the simple crustose corallines underwent many revisions, as he frequently changed his mind regarding the relative importance of the features on which he based his classification. Foslie based his generic classification mainly on sporangial features, while his subgeneric definitions were usually based on thallus structure, mainly whether the thallus was mono- or polystromatic.

Summaries of Foslie's principal systems of classification are shown in Tables 1 and 3 and a list of the species he mentioned together with their present generic classification in Table 4. The two constant features were:

1. The separation of *Melobesia membranacea* from all the other simple crustose species on the basis of its many-pored, sporangial conceptacle roof.
2. The position of *Fosliella farinosa* (as *Melobesia*) in *Melobesia* subgenus *Eumelobesia*. Foslie (1905*a*) defined *Melobesia* subgenus *Eumelobesia* as possessing trichocytes, as opposed to subgenus *Heteroderma* which lacked them. Eventually (Foslie, 1909) *Heteroderma* was elevated to generic rank and is essentially the same genus as *Pneophyllum*, although Foslie defined the genus as lacking trichocytes. Trichocytes, in Foslie's sense, however, were the terminal trichocytes of *F. farinosa*. He did not recognise intercalary trichocytes as such, although he mentioned the presence of hyaline cells in several *Heteroderma* species which would now be recognised as intercalary trichocytes. The name *Pneophyllum* has priority over *Heteroderma* on the grounds of publication date. In addition the latter is a later homonym (Stafleu *et al.*, 1978: 59) of the lichen genus *Heterodermia* Trevisan (1868), this being an orthographic variant.

C.-A. Picquenard

While working at Concarneau, Picquenard rearranged the Crouans' herbarium. He partly remounted the specimens and made catalogues of much of the material, including the red algae (Picquenard, 1912*b*). He also examined and redescribed the curious species *Hapalidium callithamnioides* P. Crouan & H. Crouan (Picquenard, 1912*a*). He came to the conclusion, like Foslie (1900*a*), that it was probably not a coralline but allied to *Rhodochorton*. He erected a new genus, *Guerinea,* for this species, but made no final decision as to its systematic position in the

Fig. 4 From Rosanoff (1866).

PLANCHE III.

Fig. 1. – Fructification tétrasporique du *M. membranacea*, coupe verticale. (Grossissement de 350 diamètres). **Fig. 2.** – *Melobesia farinosa* sur le *Fucus serratus*. (Grandeur naturelle). **Fig. 3.** – Un hétérocyste du *M. farinosa* (sur *Fucus serratus*). Les deux cellules frondales situées devant l'hetérocyste, montrent la copulation; les parois (la coupe n'est pas désincrustée), offrent une granulation assez fine; la face inférieure des parois de l'hétérocyste est recouverte d'une couche épaisse de chaux carbonatée. Dans sa partie postérieure, cette couche forme une élévation circulaire, proéminente à l'intérieur de la cellule. (Gross. de 640 diam.). **Fig. 4.** – Deux hétérocystes vus d'en haut et entourés du tissu frondal, dont les cellules montrent une copulation très abondante; on voit même 3 à 4 cellules, situées transversalement l'une à côté de l'autre, former une cavité commune. (Gross. de 600 diam.). **Fig. 5.** – Partie initiale d'une fronde de *M. farinosa*; les cellules sont ici plus ou moins carrées (1). (Gross. de 350 diam.). **Fig. 6.** – Une partie du bord d'une fronde de *Melob. farinosa* désincrustée. On voit très bien la disposition des cellules corticales par rapport aux cellules frondales et aussi la ramification des séries cellulaires. (Gross. de 600 diam.). **Fig. 7.** – Coupe verticale et radiale de la fronde du *Melob. farinosa* (sur *Fucus serratus*). On voit sur la coupe des parois, les stries radiales par rapport au centre de la cellule. On voit aussi les pores existant entre les cellules frondales et aussi entre celles – ci et les cellules corticales. (Gross. de 320 diam.). **Fig. 8.** – Une pareille coupe désincrustée. (Gross. de 320 diam.). **Fig. 9.** – Coupe centrale d'un cystocarpe de *Melob. farinosa.* (Gross. de 350 diam.). **Fig. 10.** – Une partie de la fronde adulte du *M. farinosa.* (Gross. de 40 diam.). **Fig. 11.** – Cette figure montre la ligne de confluence de deux prolifications voisines de la fronde du *M. farinosa*. **Fig. 12.** – Coupe verticale et tangentielle de la fronde du *Melob. farinosa*; on voit la copulation de deux cellules frondales. Les cellules frondales s'allongent dans les excavations de la surface du substratum. (Gross. de 350 diam.). **Fig. 13.** – Préparation analogue à celle de la fig. 6, mais avant la désincrustation: les parois des cellules apparaissent rayées dans deux directions se croisant sous un angle inféricur à 90°.

(1) Il faut faire remarquer que, généralement dans toutes les espèces de *Melobesia*, les cellules frondales qui constituent la fronde initiale, circulaire, sont plus ou moins isodiamétriques, et qu'au dessus de beaucoup d'entre elles on ne voit pas de cellules corticales.
Ces élévations circulaires, qu'on voit dans les cellules terminales, me semblent être formées, en grande partie, de chaux carbonatée, car elles disparaissent après l'action d'un acide. (Gross. de 600 diam.).

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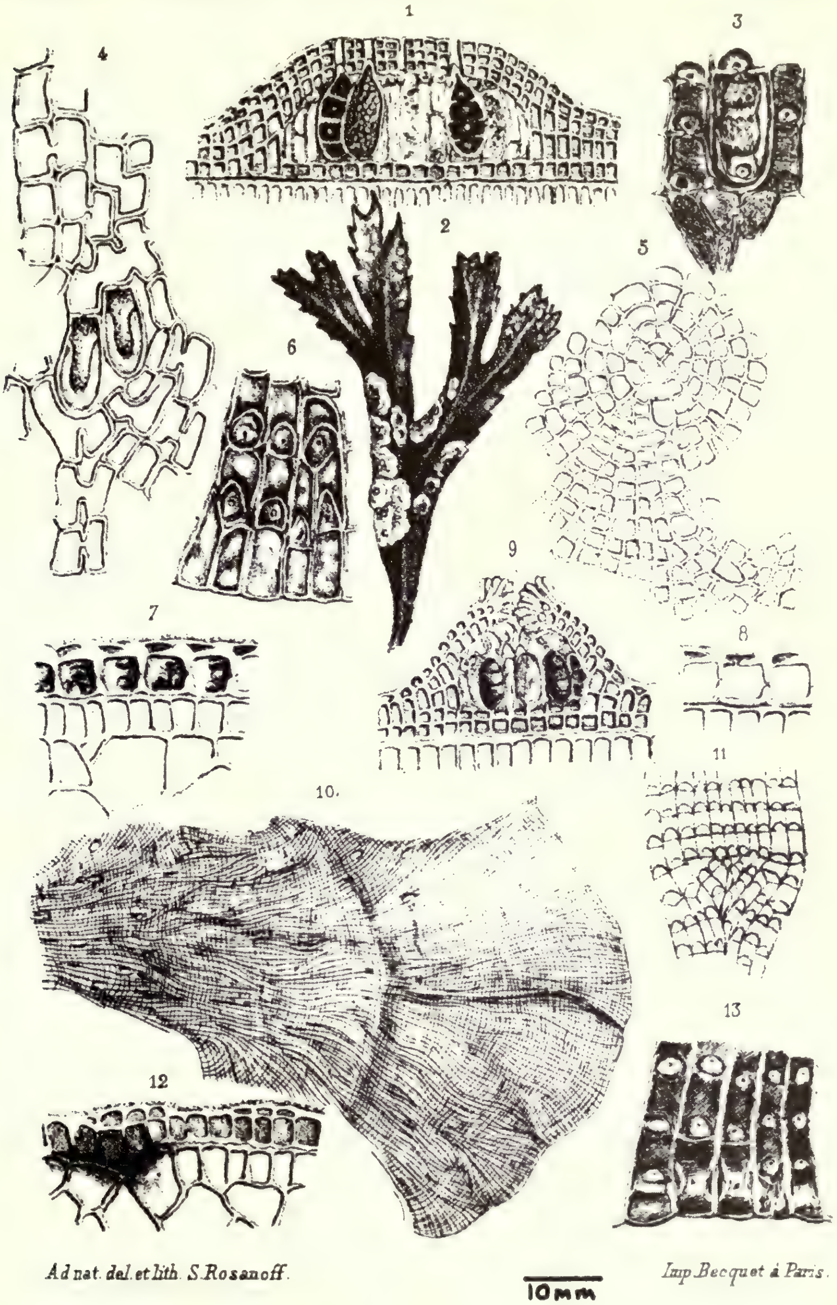
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Ad nat. del. et lith. S. Rosanoff. Imp. Becquet à Paris.

Florideophyceae. I examined material of this species at both Concarneau (CO) and Paris (PC) and found it to be the creeping form *Pneophyllum confervicolum* f. *minutulum* (*q.v.*).

M. A. Howe

Howe considered that *Melobesia* had to be typified by *M. membranacea* (Esper) Lamouroux and was, therefore, a lithothamnioid genus with many-pored roofs on the sporangial conceptacles. A new generic name had to be found for the genus of simple crustose corallines, such as *M. farinosa,* with secondary cell fusions and sporangial conceptacle roofs with a single pore. Howe (1920) proposed the name *Fosliella* to designate Foslie's *Eumelobesia* (Foslie, 1905*b*) which (in that publication) contained only *M. farinosa* sensu Lamouroux. However, although Foslie restricted *Eumelobesia* to monostromatic plants bearing trichocytes, Howe also included *M. lejolisii* and *M. chamaedoris,* both of which were considered to be without trichocytes, while *M. chamaedoris* was also 'polystromatic'.

It is proposed, therefore, that Howe's genus *Fosliella* be emended to include only species with secondary lateral cell fusions, single-pored sporangial conceptacles, and terminal hypothallial trichocytes. As has been discussed, species with intercalary or no trichocytes are classified in *Pneophyllum* Kütz.

W. A. Setchell and L. R. Mason

Setchell & Mason (1943) investigated an American alga which had been identified as *Dermatolithon pustulatum,* and concluded that it was not a *Dermatolithon* at all; they reclassified it as *Heteroderma nicholsii*. This led them to redefine the genus *Heteroderma* Foslie to include all oligostromatic species (i.e. with a thin thallus), without either trichocytes or a palisade hypothallus and with single-pored conceptacles. They designated *H. subtilissima* (Foslie) Foslie as the type species, without actually seeing a specimen. Recent examination of the type specimen from Herb. Foslie (TRH) shows it to be a minute *Pneophyllum* growing on *Corallina* from Papua.

Mason (1953) did not propose any further name changes although she suggested that the generic name *Fosliella* be restricted to species with trichocytes whether terminal or intercalary. She gave a clear account of the nomenclatural problems connected with the simple crustose

Fig. 5 From Rosanoff (1866).

PLANCHE IV.

Fig. 1. – Une partie du bord de la fronde représentée dans la fig. 10 de la pl. III. (Grossissement de 320 diamètres). **Fig. 2.** – Jeune fronde du *Melobesia pustulata*. (Gross. de 40 diam.). **Fig. 3.** – Etat plus développé de la même espèce. (Gross. de 40 diam.). **Fig. 4.** – Frondes de *Melob. macrocarpa* (sur *Phyllophora rubens*). On voit que la plupart des frondules réniformes ont leur incisure dirigée du côté inférieur de la fronde du substratum. (Grandeur naturelle). **Fig. 5.** – Coupe perpendiculaire au substratum d'une fronde de *Melob. macrocarpa.* (Gross. de 350 diam.). **Fig. 6.** – Une pareille coupe, menée tangentiellement. (Gross. de 350 diam.). **Fig. 7.** – Une partie de la membrane cellulaire du *Melob. macrocarpa*, montrant une ponctuation régulière. (Gross. de 1050 diam.). **Fig. 8.** – Trois cellules frondales du *M. macrocarpa*, vues d'en haut. Leurs parois supérieures sont très nettement ponctuées. L'incrustation très forte et la couche de chaux carbonatée qui tapisse la face intérieure des cellules frondales, rend leurs cavités plus ou moins arrondies. (Gross. de 1050 diam.). **Fig. 9.** – Coupe verticale et centrale d'un cystocarpe du *M. coronata*, (sur *Pollexfenia pedicellata*). (Gross. de 200 diam.). **Fig. 10.** – Coupe verticale et centrale d'un cystocarpe de *M. farinosa*. **Fig. 11.** – Etat jeune d'un sporange de *M. macrocarpa*, entouré des paraphyses. La cellule-mère est remplie d'un contenu incolore plein de vacuoles, et on voit le commencement de la division transversale. (Gross. de 600 diam.). **Fig. 12.** – État plus avancé du sporange; le contenu est coloré en rose brunâtre clair; les petites vacuoles ont disparu, et on ne voit que la disposition du contenu granuleux en réseau; Dans le voisinage de la cloison, qui se forme, se trouve (dans chaque loge) une vacuole elliptique, avec un nucleus excentrique. (Gross. de 600 diam.). **Fig. 13.** – Un sporange, qui s'est déjà divisé en deux loges dont le contenu est granuleux et rose intense. (Gross. de 600 diam.). **Fig. 14.** – Plusieurs paraphyses d'un cystocarpe de *Melob. macrocarpa*; leur sommet est épaissi, mamilliforme et leur contenu offre une disposition en spirale. Deux des paraphyses offrent des trous à leurs sommets. (Gross. de 600 diam.). **Fig. 15.** – Coupe verticale et centrale d'un cystocarpe de *Melob. macrocarpa.* (Gross. de 200 diam.). **Fig. 16.** – *a, b.* Sporanges, qui commencment à s'élever du fond d'un cstocarpe. **Fig. 17.** – Sporanges du *M. macrocarpa*, pris dans un échantillon desséché; *a* – vus de face, *b* – vus de côté. **Fig. 18.** – *a, b,* deux sporanges de la même espèce extraits d'un échantillon desséché. **Fig. 19.** – Une partie de la fronde désincrustée du *M. macrocarpa*; les cellules corticales sont très apparentes. **Fig. 20.** – Formation des paraphyses dans le *Melob. macrocarpa*; les cloisons inclinées transversales commencent à se dédoubler, les longues cellules montrent la ponctuation régulière: *a* avant, et *b* après la désincrustation. Les cellules de la couche, qui sert de base aux futures paraphyses, ont les, parois verticales très épaisses dans leur moitié inférieure et minces dans la moitié supérieure. La partie mince correspond, selon moi, à l'étendue dans laquelle s'est fait l'accroissement dans le sens vertical. (Gross. de 600 diam.).

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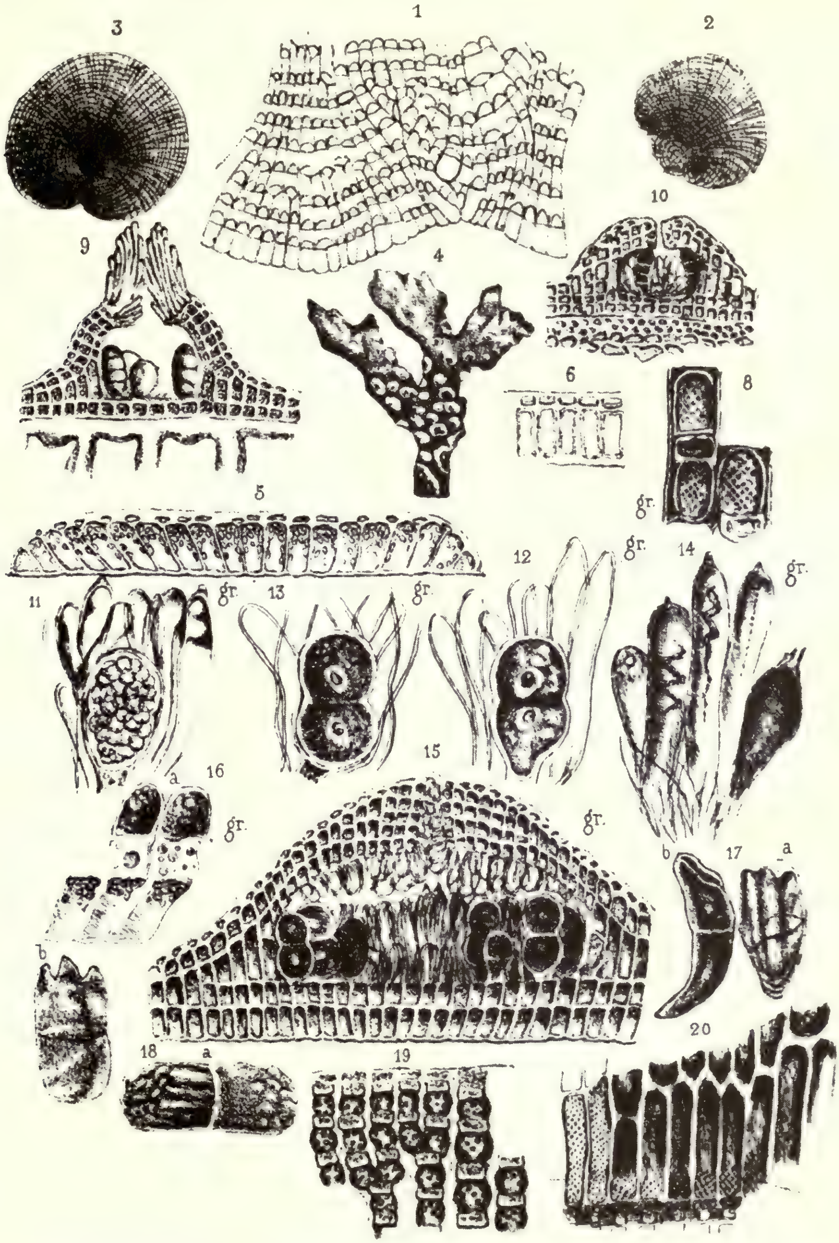
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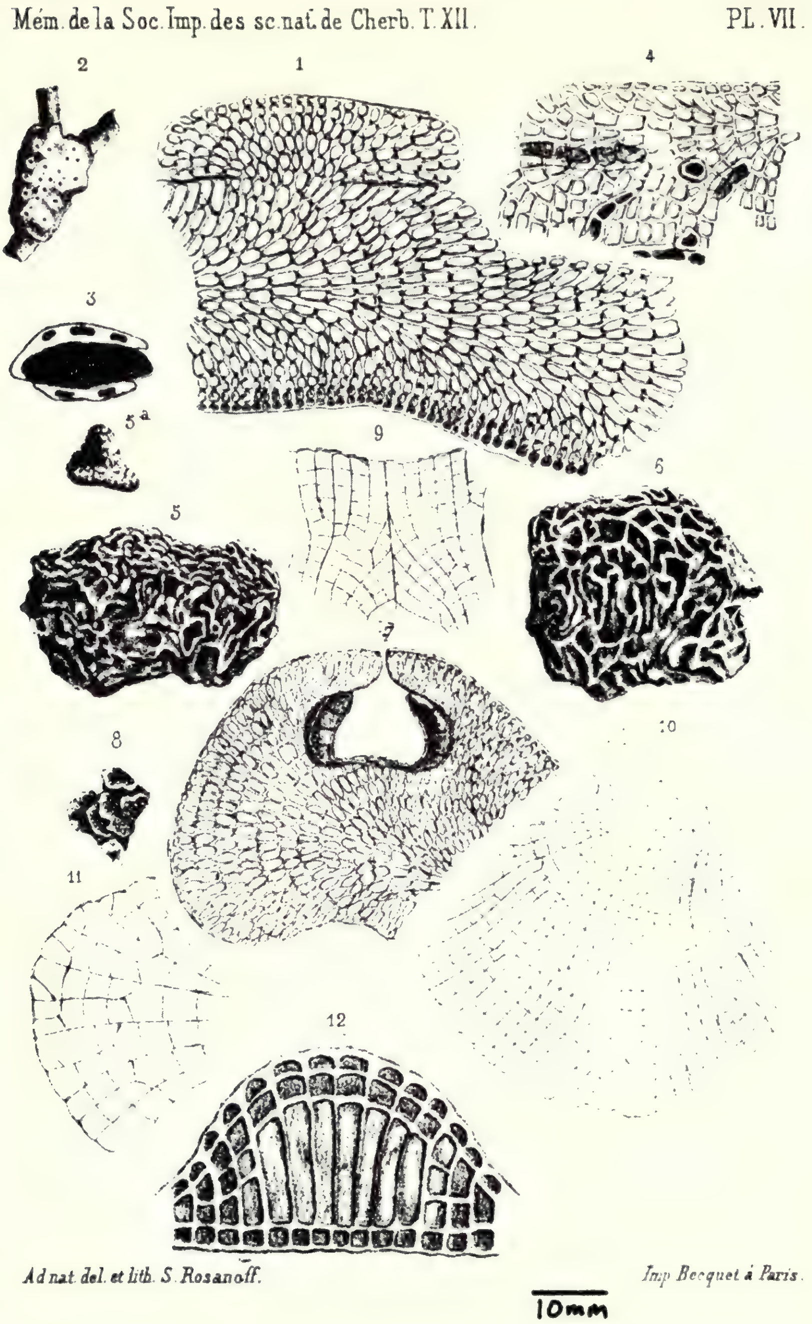
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Fig. 6 From Rosanoff (1866).

Planche VII.

Fig. 9. – La ligne de rencontre de deux ramules de la fronde du *Melobesia Lejolisii*. **Fig. 10 et 11.** – Partie des frondes du *Melob. Lejolisii*. **Fig. 12.** – Cystocarpe atrophié du *Melobesia farinosa*.

Table 2 To show names under which specimens pertaining to *Pneophyllum rosanoffii, P. lejolisii,* and *P. concollum* have been published. (Initials indicate herbaria examined.)

Publication	*P. rosanoffii* (with ostiolar filaments)	*P. lejolisii* (with flat-topped conceptacles)	*P. concollum* (with ostiolar collar)
Areschoug, 1847, 1852		*Melobesia membranacea* CHE PC	
Areschoug, 1875		*M. lejolisii* CHE PC	
Kützing, 1869	*M. farinosa* L		
Harvey, 1849, 1851		*M. membranacea?*	
Le Jolis, 1863	*M. farinosa* CHE		
Rosanoff, 1866	*M. lejolisii* pro parte CHE	*M. lejolisii* pro parte CHE	*M. lejolisii* pro parte? *M. rosea* CHE
Weber van Bosse, 1886		*M. lejolisii* L	
Lloyd no. 339 (1886)		*M. membranacea* CO	
Johnson and Hensman (1899)	*M. lejolisii*		
Foslie (1905*a*)	*M. lejolisii* f. *typica*	*M. lejolisii* f. *typica*	
Rosenvinge (1917)	*M. lejolisii* pro parte C	*M. lejolisii* pro parte C	
Suneson (1937, 1943)		*M. lejolisii*	

Table 3 Foslie's principal systems of classifying simple crustose corallines.*

Genus	Subgenus	Species
FOSLIE 1898*a* Systematical survey of the Lithothamnia		
Melobesia Lamour. emend Single orifice, with paraphyses		*M. pustulata* Lamour.
Choreonema Schm. emend. Single orifice, no paraphyses	*Heteroderma* Fosl. mscr. Thallus crust-like	*C. Notarisii* (Duf.) Fosl. mscr.
	Chaetolithon Fosl. mscr. Parasitic, with rhizoids	*C. Thuretii* (Born.) Schm.
Lithothamnion Phil. emend. Numerous orifices	*Eulithothamnion* Fosl.	*L. corticiformis* (Kütz.) Fosl. mscr.
FOSLIE 1898*b* List of species of the Lithothamnia		
Melobesia Lamour. emend. (Gen. *Choreonema* in 1898a) Single orifice, no paraphyses	*Eumelobesia* Fosl. mscr. Monostromatic	*M. farinosa* Lamour. *M. callithamnioides* Cr. *M. coronata* Rosan. *M.confinis* Cr. *M. confervoides* (Kütz.) *M. hildenbrandtioides* (Cr.) *M. zonale* (Cr.) *M. coccinea* (Cr.)

* all authorities as written by Foslie.

Table 3 – *cont.*

Genus	Subgenus	Species
	Heteroderma Fosl. Polystromatic	*M. inaequilaterata* Solms. *M. Novae Zelandiae* Heydr. *M. rosea* Kütz. *M. Notarisii* Duf. *M. prototypus* Fosl. *M. Laminariae* Cr. M. *Corallinae* Cr. *M.? myriocarpa* Fosl. *M. Cystosirae* Hauck. *M.? rhizomae* (Heydr.)
Choreonema Schm. Parasitic		*C. Thuretii* (Born.) Schm.
Dermatolithon Fosl. mscr. (Gen. *Melobesia* in 1898*a*) Single orifice, with paraphyses		*D. pustulatum* (Lamour.) Fosl. mscr. f. *bispora* Fosl. mscr. (*M. pustulata* Lamour. s.s.) f. *macrocarpa* (Rosan.) Fosl. mscr. *D. Lejolisii* (Rosan.) Fosl.mscr. *D. hapalidioides* (Cr.) Fosl. mscr.
Lithothamnion Phil. emend.	*Epilithon* (Heydr.) Fosl. mscr. Monostromatic	*L. membranaceum* (Esper) Fosl. mscr. *L. corticiforme* (Kütz.) Fosl.
FOSLIE 1900*b* Revised systematical survey of the Melobesieae		
Melobesia Lamour. emend. Conceptacles superficial or slightly immersed or conical, disc plain and connected to roof only at first	*Eumelobesia* Fosl. Monostromatic	*M. farinosa* Lamour. *M. callithamnioides* Falkbg. nec. Crn. (M. farinosa f.?) *M. lejolisii* Rosan. *M. confervicola* (Kütz.) Fosl. *M. caspica* Fosl. *M.? Novae Zelandiae* Heydr.
	Heteroderma Fosl. Polystromatic	*M. Corallinae* Solms (nec. Crn.?) *M. coronata* Rosan. *M. canescens* Fosl. *M. zonalis* (Crn.) Fosl. *M.? Cystoseirae* Hauck
Lithophyllum Phil. emend. Conceptacles scarcely raised, sporangial disc overarched, initially attached to roof then freed, roof usually finally decorticated	*Carpolithon* Fosl. Conceptacles scarcely raised, roof finally decorticated, disc less overarched	*L. decipiens* Fosl. *L. discoideum* Fosl.
	Lepidomorphum Fosl. Conceptacles immersed or sub-prominent-convex, roof finally decorticated, disc ± overarched and connected to roof	*L. zostericolum* Fosl. f. *tenuis* Fosl. f. *mediocris* Fosl. *L. papillosum* (Zan.) Fosl.
Dermatolithon Fosl. Conceptacles sub-immersed or conical, disc plain, club-shaped free paraphyses		*D. pustulatum* (Lamour.) Fosl. f. *typica* f. *crinita* Möb. *D. macrocarpum* (Rosan.) Fosl. f. *faeroënsis* Fosl.

		f. *Laminariae* (Crn.) Fosl.
		D. hapalidioides (Crn.) Fosl.
		f. *typica* (Inc. *Melob. simulans* Crn.)
		f. *confinis* (Crn.) Fosl.
		D.? adplicitum Fosl. (*D. hapalidioides* f.?)
		D.? prototypus Fosl.
Lithothamnion Phil. emend.	*Epilithon* (Heydr.) Fosl.	*L. membranaceum* (Esper) Fosl.
		L. corticiforme (Kütz.) Fosl.

FOSLIE 1905*a* Remarks on northern Lithothamnia
FOSLIE 1905*b* New Lithothamnia and systematical remarks (1905*b* additions in brackets)

Melobesia Lamour.	*Eumelobesia* Fosl. monostromatic, epithallium present, heterocysts present	*M. farinosa* Lamour. f. *typica* f. *borealis* Fosl. mscr. f. *callithamnioides* (Falkbg.) Fosl. (f. *mauritiana* Fosl. mscr.)
	Heteroderma Fosl. monostromatic, epithallium present or absent, heterocysts absent	*M. lejolisii* Rosan. f. *typica* f. *limitata* Fosl. mscr. *M. minutula* Fosl. f. *typica* f. *lacunosa* Fosl. mscr. (*M. Cymodoceae* Fosl.) (*M. triplex* Heydr. = *M. Cymodoceae* Heydr.?) (*M. coronata* Rosan.) (*M. rugulosa* Setch. et Fosl.) (*M. subtilissima* Fosl.) (*M. Novae Zelandiae* Heydr.?)
Lithophyllum Phil.	*Dermatolithon* Fosl.	p. 117 *L. pustulatum* (Lamour.) Fosl. f. *australis* Fosl. mscr. f. *intermedia* Fosl. mscr. f. *macrocarpa* (Rosan.) Fosl. f. *Corallinae* (Crn.) Fosl. mscr. f. *Laminariae* (Crn.) Fosl. mscr. p. 128 changed this classification to:– *L. pustulatum* (Lamour.) Fosl. *L. macrocarpum* (Rosan.) Fosl. mscr. f. *intermedia* Fosl. mscr. f. *faeröensis* Fosl. mscr. f. *Laminariae* (Crn.) Fosl. mscr. *L. hapalidioides* (Crn.) Fosl. f. *typica* f. *confinis* (Crn.) Fosl. (*L. canescens* Fosl.) (*L. prototypum* Fosl.) (*L. tumidulum* Setch et. Fosl.) (*L. polycephalum* Fosl.)

corallines, and in particular of the history of all the changes that had occurred to *Heteroderma* in the course of Foslie's publications.

W. H. Adey and P. J. Adey

On the basis of his examination of Foslie's herbarium in Trondheim, Adey (1970) considered that simple crustose corallines with lateral cell fusions and single-pored conceptacles should not

Table 4 Genera to which species listed by Foslie now belong.

D.	*Adplicitum*
D.	*bermudense*
P.	*Callithamnioides*
D.	*Canescens*
*D.?	*Caspica* (or *Litholepis*?)
P.	*Caulerpae*
P.	*Chamaedoris*
M.	*coccinea*
P.	*confervicola*
D.	*confinis*
P.	*confervoides*
D.	*conspectum*
D.	*corallinae*
P.	*coronata*
D.	*corticiformis*
P.	*Cymodoceae*
D.	*Cystoseirae*
Ps.	*decipiens*
Ps.	*discoideum*
D.	*dispar*
P.	*explanata*
F.	*farinosa*
M.	*galapagense*
P.	*Gibbsii*
D.	*hapalidioides*
M.	*hildenbrandtioides*
F.?	*inaequilaterata*
D.	*Laminariae*
P.	*lejolisii*
P.	*lepturum*
P.	*limitata*
D.	*macrocarpa*
M.	*marginata*
P.	*mauritiana*
M.	*mediocris*
L.	*melobesioides*
M.	*membranacea*
P.	*minutula*
P.	*myriocarpa*
M.	*Notarisii*
P.?	*Novae Zelandiae*
D.	*papillosum*
D.	*polycephalum*
D.	*prototypus*
D.	*pustulatum*
D.	*rasile*
P.?	*rhizomae*
M.	*Rosanoffii*
P.	*rosea*
P.	*rugulosa*
P.	*Sargassi*
P.	*subtilissima*
C.	*Thuretii*
P.	*triplex*
D.	*tumidulum*
P.	*zonale*
P.	*zostericola*

C. = *Choreonema* Schmitz
D. = *Dermatolithon* Foslie
F. = *Fosliella* Howe
M. = *Melobesia* Lamouroux
N. = *Neogoniolithon* Setchell & Mason
P. = *Pneophyllum* Kützing
Ps. = *Pseudolithophyllum* sensu Lemoine
L. = *Lithoporella* Foslie

be divided into separate genera on the basis of the presence or absence of trichocytes. He referred them all to *Heteroderma* Foslie. In 1973, however, Adey & Adey described two new species of *Fosliella,* both of which possessed intercalary trichocytes.

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* usually given as *Litholepis* but Zinova (1967) refers it to *D. caspicum* (Foslie) Zaberzh.

Summary

The solutions arrived at in the present investigation are:

(1) *Melobesia membranacea* (Esper) Lamouroux should remain the type species of *Melobesia* Lamouroux (1812) since I consider that the drawing by Esper (1806) which Lamouroux cited in his description illustrates the present species.

(2) The name *Fosliella* M. Howe (1920) should be restricted to species with terminal trichocytes and be typified on *F. farinosa* (Lamouroux) M. Howe. Species with intercalary trichocytes should be classified in *Pneophyllum* Kütz. (1843) and be typified on *P. fragile* Kütz.

Coralline structure

Introduction

Spore germination characteristics, thallus structure, and development as well as reproductive features of coralline algae have recently been considered in a number of publications. In particular Chamberlain (1978) discusses simple crustose corallines, while Johansen (1981) summarises current knowledge for the entire Corallinaceae. Only a brief account will, therefore, be given of those principal features which particularly appertain to *Fosliella* and *Pneophyllum*.

Spore germination

Newly released coralline spores of all types (ie. carpospores, tetraspores, and bispores) are approximately globular, deep red bodies encased in a clear coating which is presumably mucilaginous (Jones & Moorjani, 1973). As described in Chamberlain (1982) the spores, on settling, become attached to the substratum by means of an adhesive mucilage and segment to produce up to 32 cells within the confines of the original spore wall before growth of the sporeling beyond this wall commences (Figs 7, 8). This type of segmentation was described by Chemin (1937) as the *Dumontia*-type and is seen almost throughout the Corallinaceae when spores germinate under favourable conditions. A filamentous type of germination, the *Naccaria*-type, is, however, seen in parasitic and semiendophytic species (Cabioch, 1972) and in other species such as *Fosliella farinosa* when germination occurs under unfavourable conditions (Chamberlain, 1982).

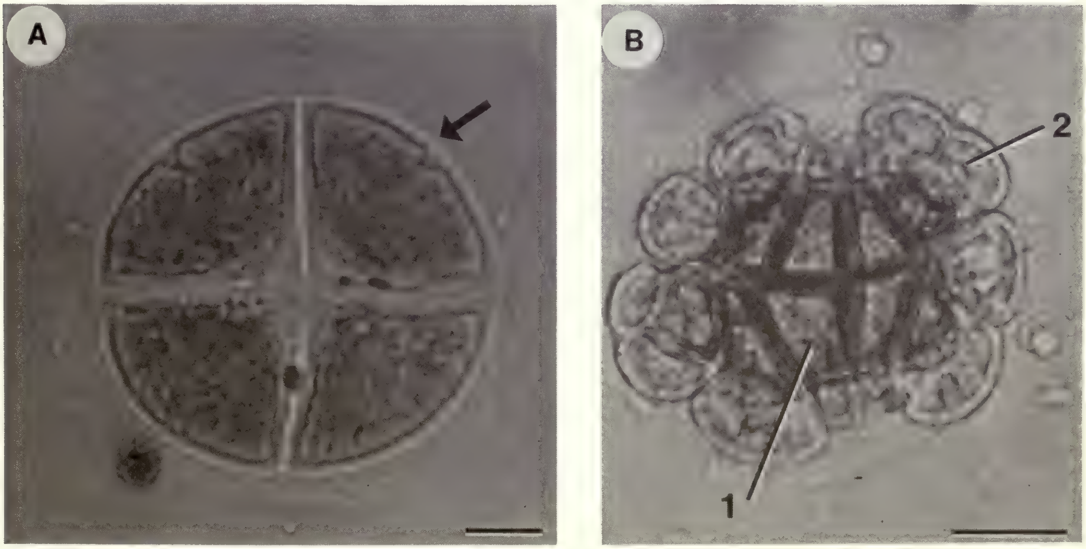


Fig. 7 Spore segmentation in *Pneophyllum* and *Fosliella*. A, Second division of *Pneophyllum lobescens* carpospore showing adhesive mucilage (arrow). Scale = 10 μm. B, *Fosliella farinosa* sporeling (from bispore) showing four-celled central element (1) and young peripheral growth (2). Scale – 20 μm.

The sequence of spore segmentation was further studied by various authors such as Chihara (1973, 1974*a*, *b*), Notoya (1974, 1976*a*, *b*), and Bressan (1980) who all recognised that particular sequences could generally be related to taxonomic groupings, particularly to the subfamily. These authors all found, however, that the simple mastophoroid species (variously attributed to the genera *Fosliella* and *Heteroderma*) showed a wide diversity of pattern. Chamberlain (1982) considered that these patterns could all be related to two fundamental types, those with a four-celled central element (Fig. 7B) to the germination disc, as found in *Fosliella*, and those with an eight-celled central element (Fig. 8), as found in *Pneophyllum* (previously including *Fosliella* spp. and *Heteroderma* spp.). This is considered to be the most consistent and fundamental character at present recognised as separating these two genera (Chamberlain, 1982).

After segmentation, peripheral growth commences (Figs 7B; 8), either all round the segmented spore to form immediately a circular disc, or from one or two points on the periphery to form fan-shaped discs, which usually, however, eventually unite into a more or less circular disc.

The vegetative thallus

Thallus components

As with the majority of red algae, the coralline thallus is fundamentally composed of filaments. The basic structure of the thallus may be seen most easily in the simple crust, but this form is not necessarily primitive and may, in some cases at least, be neotenic (cf. Cabioch, 1971*b*, 1972). The mature simple crust is generally a disc-like structure which starts as a single basal layer of radiating, calcified filaments, called the **hypothallium**, which is initiated from the periphery of the segmented spore (Figs 8; 9A) and continues to grow by the activity of peripheral apical initials (Figs 9; 10A). Each differentiated cell of the hypothallium cuts off a small, lightly calcified or uncalcified cell on the upper surface of its distal end called the **epithallial cell** (Figs 8; 9A, B; 10B, C). In the simplest forms, including all currently known species of *Fosliella* and

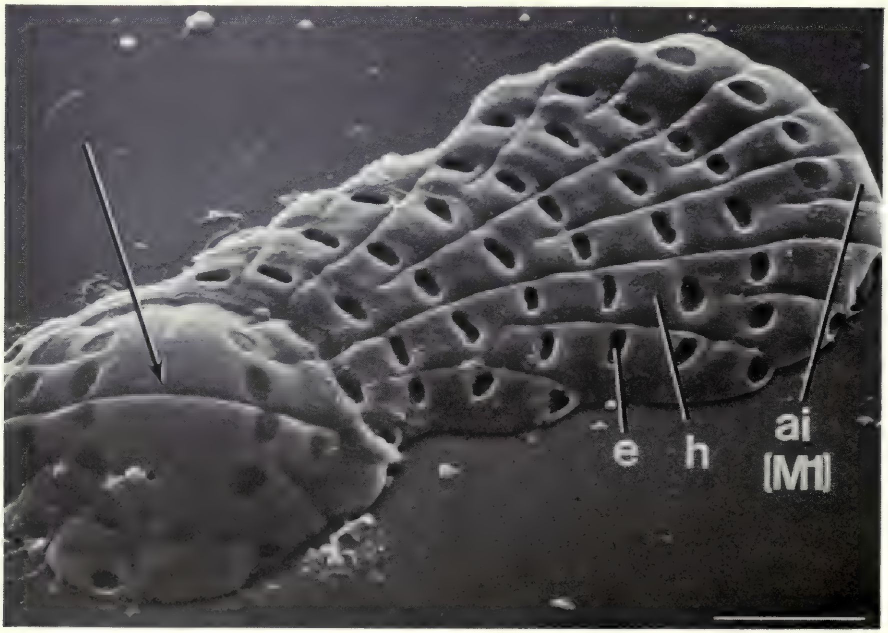


Fig. 8 Scanning electron micrograph of germinating bispore of *Pneophyllum lobescens* to show eight-celled centre (arrow) giving rise to radiating filaments of hypothallial cells produced by the apical initial which forms the first meristem; each hypothallial cell cuts off an epithallial cell. Scale = 25 μm.

some *Pneophyllum* spp., no further cell types are formed in the vegetative thallus. Many simple crustose species and all complex crusts, however, develop a third component, the **perithallium**, which lies between the hypothallium and the epithallium (Figs 9B; 10B; 11C). At its simplest, the perithallium comprises single calcified meristematic cells (subapical initials) cut off by a periclinal division from the upper side of each cell of the hypothallial filaments. In many species, however, the initials continue dividing periclinally, cutting off successive perithallial cells from their lower side (Fig. 10B) which form perithallial filaments; these may be up to twenty cells deep in *Pneophyllum* depending on the species. Perithallial and hypothallial cells often contain abundant floridean starch grains (Fig. 11B). In addition to cutting off perithallial cells towards the base of the crust the subapical initials continue (possibly throughout the life of the crust), to cut off successive epithallial cells on the crust surface, the older cell usually being sloughed off as the new one develops (Bressan *et al.*, 1981). In some complex crustose species, and very occasionally in *Pneophyllum,* the epithallial cells are not sloughed off as the new ones develop and short filaments of epithallial cells consequently occur.

It can be seen, therefore, that crust growth is accomplished by the activity of two types of meristem (Fig. 9). The hypothallium expands peripherally by the division of apical initials which collectively comprise a meristem that will be called the **first meristem** since it is the first to be initiated after spore segmentation. The epithallium and perithallium subsequently develop from the activity of intercalary, or subapical, initials which are situated between these two thallus components and which will collectively be called the **second meristem**, since it is always initiated after the hypothallial meristem. Woelkerling (1980), Johansen (1981), and Turner & Woelkerling (1982) refer to the first meristem as the primary meristem and the second meristem as the secondary (Woelkerling, 1980; Turner and Woelkerling, 1982) or intercalary (Johansen, 1981) meristem, by analogy with phanerogams. I think it preferable, however, to limit the analogy solely to the sequence of development without making precise terminological comparisons with higher plants, since the basically filamentous structure of the algal thallus is quite different from the phanerogam thallus organisation.

Cell connections

The successive cells of hypothallial, epithallial, and perithallial filaments are joined by normal red algal pit connections (Figs 9B; 10B, C; 11C), the pit plugs of which (Pueschel & Cole, 1982) have recently been shown to be of a particularly elaborate nature (Fig. 11A). A characteristic of the Corallinaceae is the development of secondary lateral synapses between contiguous cells of

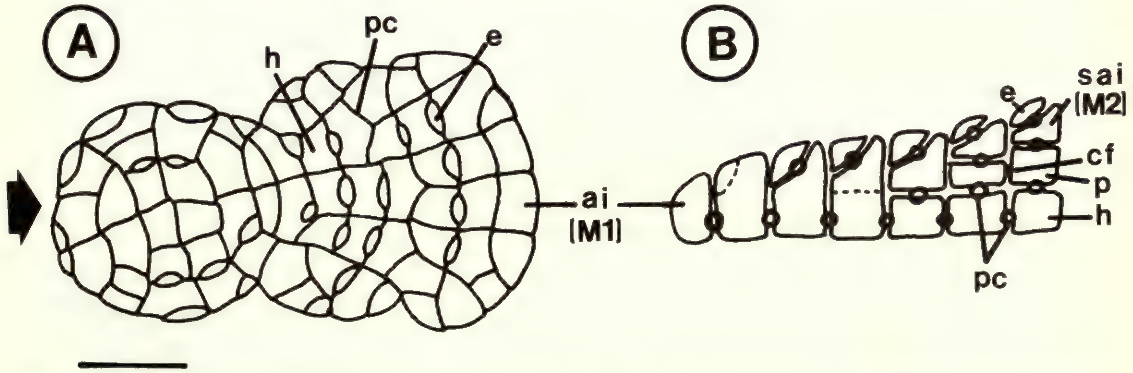


Fig. 9 Thallus features in *Fosliella* and *Pneophyllum.* A, Diagrammatic surface view of *Pneophyllum lobescens* sporeling (arrow = original spore). Scale = 50 μm. B, Diagrammatic radial VS of *Pneophyllum* crust periphery (redrawn after Cabioch, 1972).

Figures 8 and 9 represent the following features: h = hypothallial cells forming the prostrate radiating filaments; p = perithallial cells of erect filaments; e = epithallial cells; ai = apical initials; M1 = first meristem composed of apical initials; sai = subapical initial; M2 = second meristem composed of subapical initials; pc = primary pit connection; cf = cell fusion.

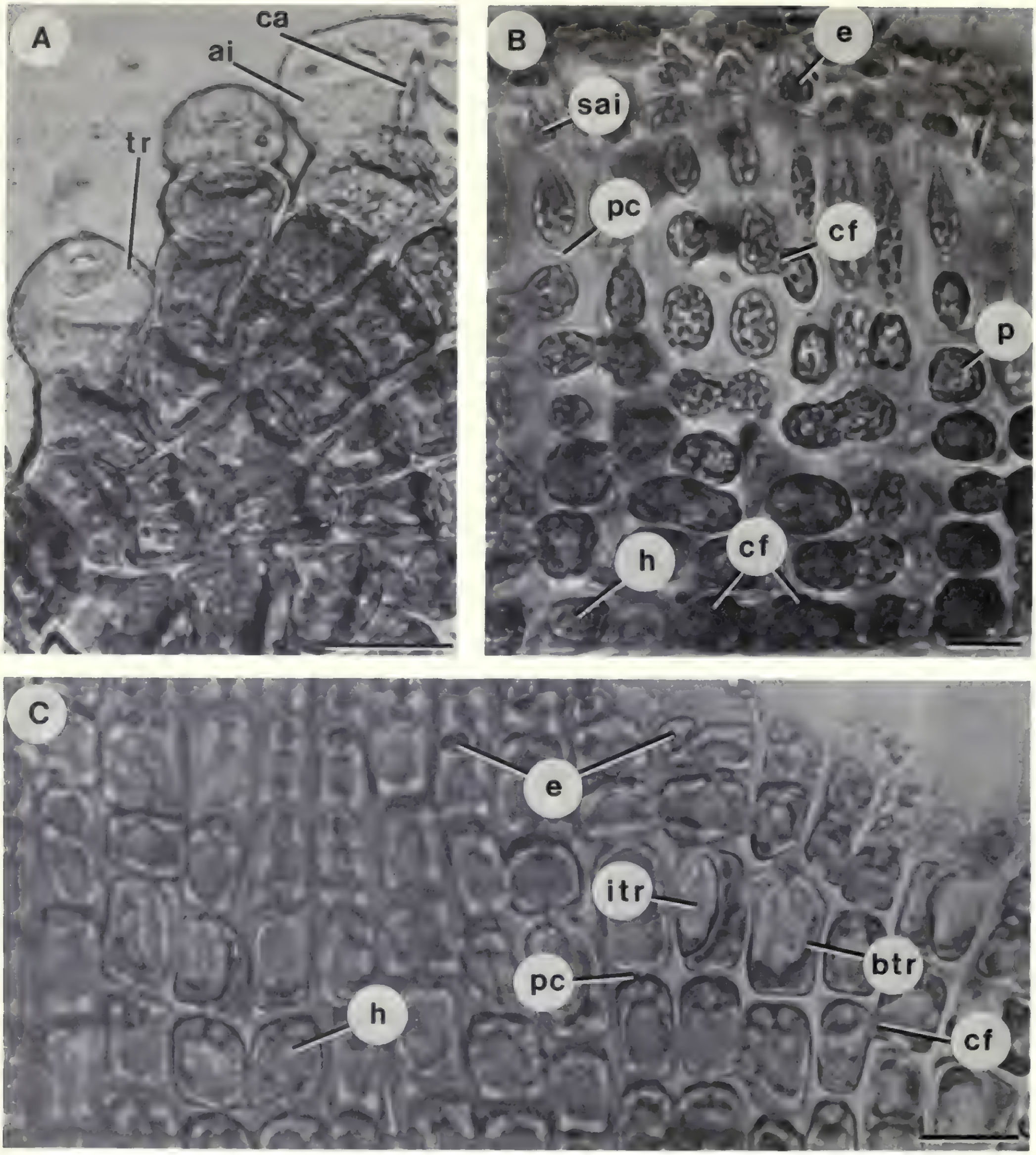


Fig. 10 Thallus components of *Fosliella* and *Pneophyllum*. A, *Fosliella farinosa* sporeling to show peripheral initiation of terminal trichocyte (tr), apical initial (ai) and onset of calcification (ca). Scale = 20 μm. B, Vertical section of *Pneophyllum plurivalidum* crust to show perithallial (p) and hypothallial (h) filaments, epithallial cells (e), pit connections (pc) between successive perithallial cells, fusions (cf) between contiguous perithallial cells, and hypothallial cells and subapical initials (sai). Scale = 10 μm. C, Surface view of *Pneophyllum rosanoffii* crust to show hypothallial cells (h), epithallial cells (e), branch cell intercalary trichocyte (btr), intrafilament intercalary trichocyte (itr), pit connections (pc), and cell fusion (cf). Scale = 25 μm.

hypothallial and perithallial filaments. These synapses are described in detail by Cabioch (1970*b*, 1971*b*) and may be in the form of secondary pit connections similar to the primary pit connections mentioned above, or fusions in which the walls of adjoining cells decompose to form coenocytes (Figs 9B, 10B, C). The type of secondary synapse present is considered to be of phylogenetic significance and in *Fosliella* and *Pneophyllum* only cell fusions are seen.

Trichocytes

A feature of many members of the Corallinaceae is the presence of trichocytes (i.e. hair-bearing cells) in the thallus; Cabioch (1968, 1970*a*, *b*, 1971*b*) comprehensively describes the diversity of trichocytes in the Corallinaceae so that only the forms found in simple crusts (as investigated by myself) are considered here. The trichocytes which occur in hypothallial cells in the crust periphery are of two types: (1) in *Fosliella* the **terminal trichocyte** develops at the first meristem when an apical initial (Fig. 10A) becomes somewhat swollen and, when mature, divides by a tangential, more or less anticlinal wall; the centrifugal part then develops a hair. The hair is often shed quite quickly, but the trichocyte persists in the thallus and terminates the growth of the filament which bears it; contiguous thallus filaments subsequently grow round the trichocyte to continue the growth of the thallus; (2) in *Pneophyllum* trichocytes usually develop from a differentiated thallus cell (or occasionally in an apical initial) and in this case the cell divides by a radial, anticlinal wall into a pigmented part and a colourless, hair-bearing part (Fig. 10C). Since this type of trichocyte develops within a filament which grows on beyond it, it is known as an **intercalary trichocyte**: it may develop either within an unbranched length of filament (Fig. 10C) here called an **intrafilament type**, or in a filament branch cell (Fig. 10C) here designated as a **branch cell type**. In addition, large, sac-like, terminal cells bearing hairs occasionally develop in *Pneophyllum,* probably as a response to specific environmental conditions; these have been observed in *P. limitatum* by Suneson (1943, as *Melobesia*) and in *P. myriocarpum* (Chamberlain, 1982) and can be regarded as abnormal structures clearly distinguishable from the 'normal' terminal trichocytes of *Fosliella* by their large size (at least twice the length of crust cells) and lack of cross walls. The taxonomic significance of trichocytes in these genera has, as Johansen (1981) remarks, frequently been questioned, especially as their occurrence appears to depend on environmental conditions; I have confirmed (Chamberlain, 1982) that their occurrence depends on a sufficiently high temperature and light intensity and they are, for example, usually absent in winter and in deeper subtidal habitats. However, while I have never found intercalary trichocytes in the hypothallium of *Fosliella,* in *Pneophyllum* the trichocytes, when present, are normally intercalary. At the very least, therefore, I consider this a useful feature for practical generic identification.

Reproduction

Vegetative reproduction

As Johansen (1981) remarks, many coralline algae are readily capable of vegetative reproduction in that small fragments of thallus are able to reattach themselves to a substratum and regenerate. Specific vegetative reproductive organs are rare however, although propagules have been described in *Fosliella farinosa* (Solms-Laubach, 1881, as *Melobesia callithamnioides*; Coppejans, 1978) and *F. paschalis* (Hollenberg, 1970), while Suneson (1943) observed contracted protoplasts in marginal cells of *Pneophyllum limitatum* (as *Melobesia*), which he suggested might be organs of vegetative reproduction.

Conceptacles

The non-vegetative reproductive cells of all corallines are borne in protruding, more or less hemispherical, or immersed, flask-like, chambers known as conceptacles (Fig. 11F) which are formed by the growth of the vegetative thallus. Four different conceptacle types occur, containing tetrasporangia, bisporangia, carpogonia, and spermatia respectively. The carposporophyte develops within the carpogonial conceptacle after the carpogonium has been (presumably) fertilised by a spermatium although direct evidence that fertilisation occurs has yet to be obtained. Details of the mode of conceptacle development in various coralline groups are summarised by Johansen (1981). Almost all conceptacle types release spores through a single common pore, the ostiole, in the conceptacle roof; in the subfamily Melobesioideae (Fig. 16) however, tetra- and bisporangia are released through individual pores, and the conceptacle roof in this case is therefore pierced by numerous pores (see Chamberlain, 1978).

The conceptacles of *Fosliella* and *Pneophyllum* are prominent structures in species with a thin vegetative thallus but may be entirely immersed in the thicker species such as *P. plurivalidum*. Gametangial, tetrasporangial, and bisporangial conceptacles are known for most species, but bisporangial conceptacles have not yet been recorded in some of the present species such as *P. rosanoffii* and *P. sargassi*; two distinct forms of bisporangial conceptacle occur in *P. limitatum*, both bearing uninucleate bisporangia.

Garbary (1978) examined the appearance of the conceptacle in a range of articulated and crustose corallines under the S.E.M. He found that, while the conceptacle surface resembled the thallus surface in most species, in some species such as *Dermatolithon litorale* and *Fosliella farinosa*, uneven calcification of the outer cell walls occurs causing the cells to bulge outwards, thus orientating the epithallial cell in an almost horizontal position. Garbary also noted distinctive rosette-like cell patterns round the ostiole in some species.

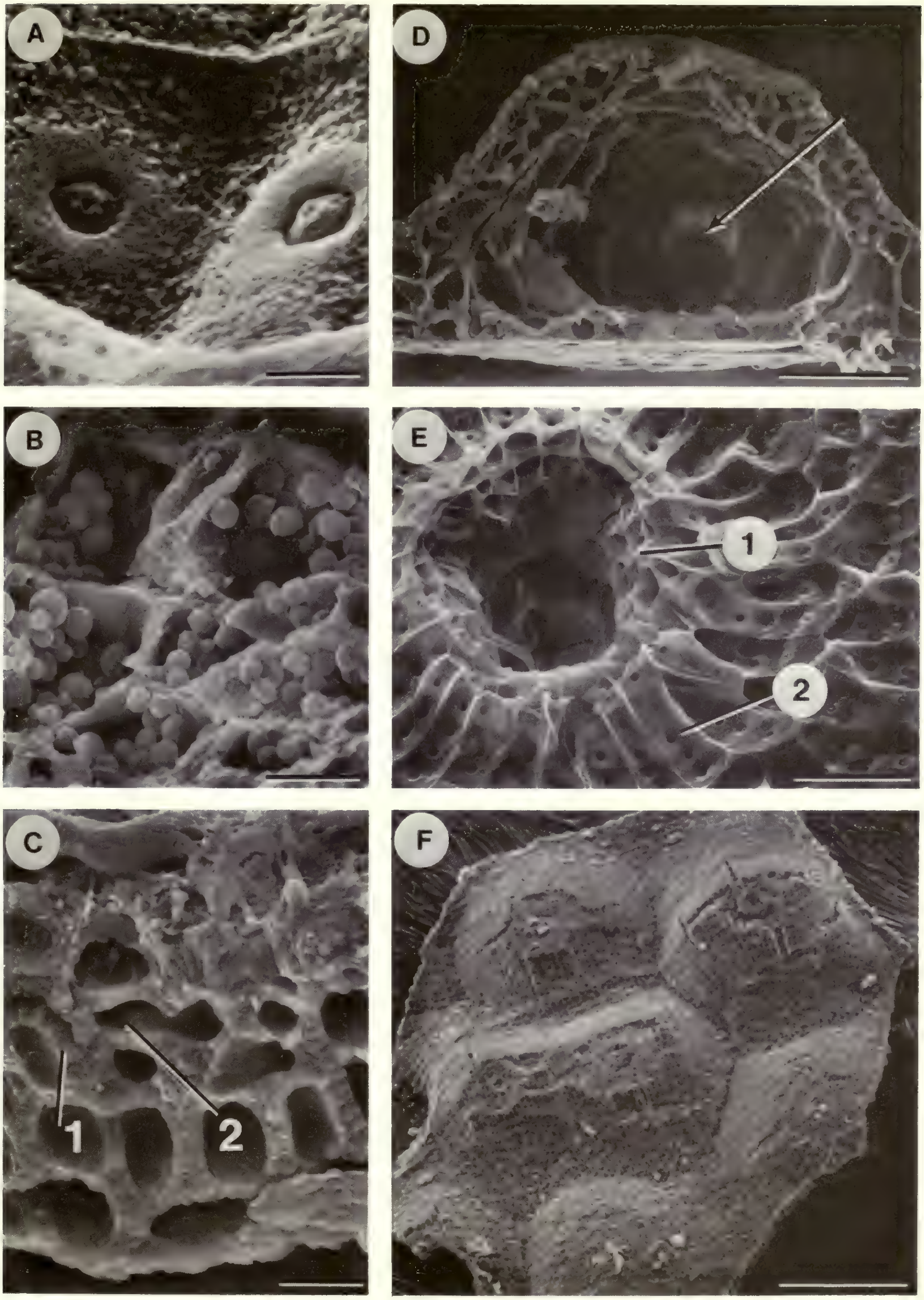
In the present investigation, the structure of the conceptacle, particularly of the ostiolar area, has been found to be of systematic significance in separating species of *Pneophyllum*. Studies on decalcified, sectioned material, in conjunction with S.E.M. studies of air and critical point dried material of the same taxon, have made it possible to follow conceptacle development and this has led to a better understanding of how the mature features should be interpreted. Many aspects of the developmental process are common to all conceptacle types and the basic principles are demonstrated for the carpogonial/carposporangial conceptacle of *Pneophyllum rosanoffii* (Figs 12A–G).

A carpogonial conceptacle of *P. rosanoffii* is initiated (Fig. 12A) when the subapical initials cut off additional perithallial cells over a circular area of crust and these perithallial cells (called cavity cells in Johansen, 1981) become vertically stretched. Fertile initials (Fig. 12A) develop centrally on the floor of the central disc and the perithallial cells above them disintegrate. In *P. rosanoffii* a ring of persisting perithallial cells surrounding the ostiole become meristematic apically (Fig. 12B) and give rise to upward and downward ostiole filaments (Fig. 12F). Eventually the perithallial cells at the periphery of the conceptacle rupture, their outer walls form a lining to the chamber which is evident in section as a thin hyaline layer (Fig. 12E) and can be seen as a smooth surface in S.E.M. preparations (e.g. in *P. myriocarpum,* Fig. 11D).

The filaments surrounding the ostiole (papillary cells in Masaki, 1968) develop in characteristic ways in different species. In the thin crusted *P. lejolisii* and deep crusted *P. microsporum*, for example, development is minimal. Upward ostiole filaments are particularly well developed in species such as *P. limitatum, P. zonale,* and *P. rosanoffii* (*q.v.*); these filaments are probably uncalcified but they nevertheless persist during S.E.M. preparation, particularly in critical point dried material. In most species a ring of downward pointing filaments surrounds the ostiole (Fig. 12F); in some species such as *P. concollum* the filament tips may become swollen. Under the S.E.M. the inside surface of the conceptacle roof of *P. zonale* (Fig. 11E) shows that while the basal parts of these filaments are heavily calcified, the tips presumably remain thin-walled and uncalcified since they have disappeared in air dried material.

Some species, in addition to producing ostiole filaments, produce filaments which form a new roof below the original crust surface as can be seen in *P. plurivalidum* (e.g. Fig. 77A). When this occurs the original crust surface sloughs off to reveal the new roof cells (e.g. in *P. zonale*, Fig. 11F), which are more or less isodiametric in most species. The upper parts of the perithallial cells which produce the ostiole filaments can often be seen as irregularly shaped structures (in *P. lobescens* for example). In air dried, S.E.M. preparations these irregular cell remnants disintegrate, leaving a pattern of pit connections (e.g. in *P. zonale*, Fig. 11E) showing where the

Fig. 11 Scanning electron micrographs to show morphological features of *Pneophyllum*. A, Pit plugs from primary pit connection of *Pneophyllum zonale*. Scale = 2 μm. B, Vertical section of *Pneophyllum zonale* crust to show the globular grains of floridean starch. Scale = 10 μm. C, Vertical section of *Pneophyllum* sp. showing heavily calcified cell walls with calcite crystals orientated at right angles to the lumen (1) and a pit connection between perithallial cells (2). Scale = 10 μm. D, Vertical section of tetrasporangial conceptacle of *Pneophyllum myriocarpum* showing the smooth lining formed from remnants of perithallial cell walls (arrow). Scale = 50 μm. E, View from below of the roof of a



bisporangial conceptacle of *Pneophyllum zonale* showing the calcified parts of downward ostiole filaments (1) and rows of pit connections marking the place at which ostiole filaments are given off by the perithallial cell (2). Scale = 25 μm. F, Bisporangial conceptacles of *Pneophyllum zonale* (critical point dried). Scale = 250 μm.

new filaments were given off. Whether or not a new conceptacle roof is formed, and the way in which the old thallus surface is shed in species which produce a new roof, has proved to be a useful taxonomic character (see page 335). While the features can only be seen clearly under the S.E.M. it is often possible to deduce information about them from vertical sections.

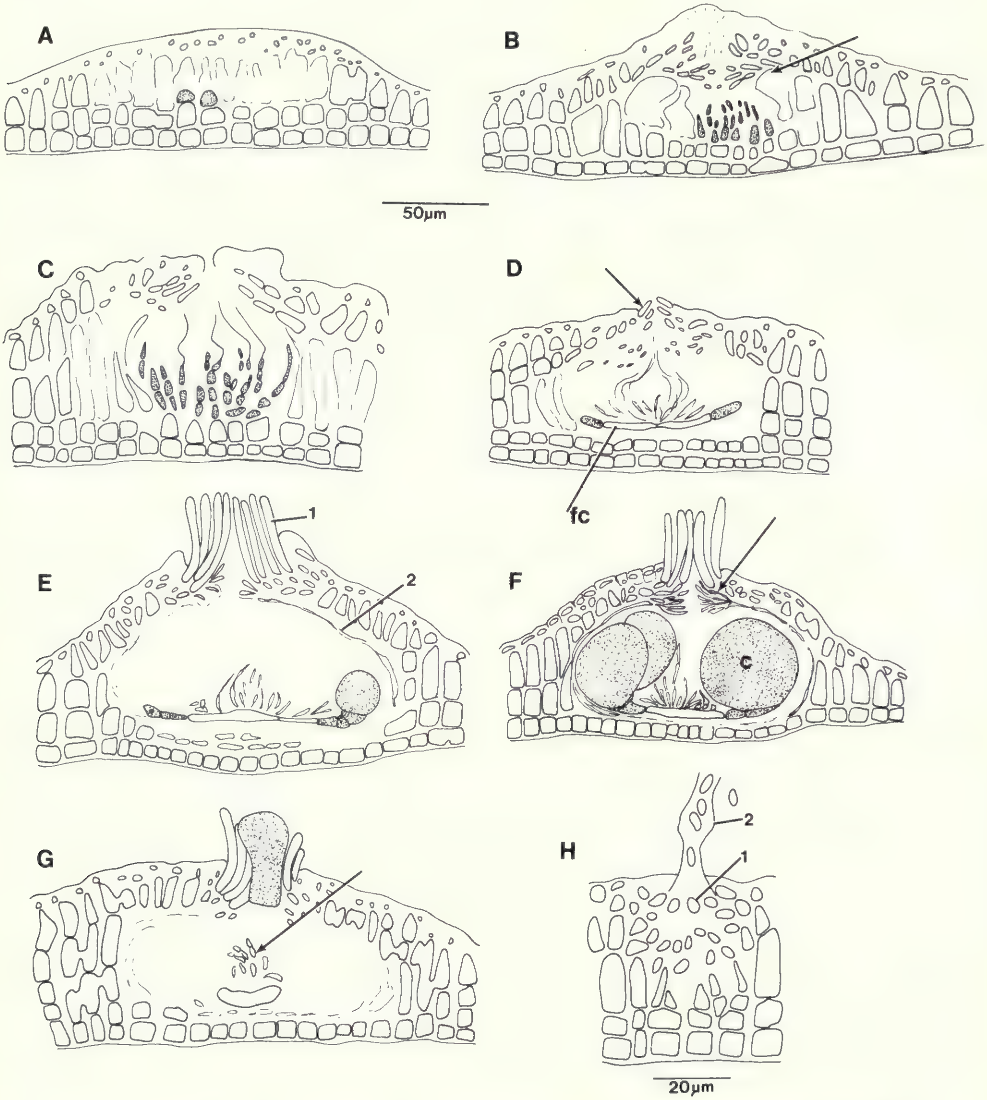


Fig. 12 Vertical sections of *Pneophyllum rosanoffii* to show structure and development. A–C, Carpogonial conceptacles. A, Initiation and stretching of perithallial cells and appearance of fertile initials (shaded). B, enlargement of perithallial cells and initiation of roof and ostiole filaments (arrow); young procarps developing (shaded). C, Mature procarps (shaded) and further growth of roof. D, Appearance of fusion cell (fc) and initiation of peripheral gonimoblast filaments (shaded); early stage in growth of upper ostiole filaments (arrow). E–G. Carposporangial conceptacles. E, Growth of peripheral gonimoblast filaments (shaded); maturation of upward ostiole filaments (1). Perithallial cells now form a conceptacle lining (2). F, Maturation of carposporangia (c) and downward ostiole filaments (arrow). G, Dispersal of final carpospore through ostiole and senescence of fusion cell and remaining procarp remanants (arrow). H, Spermatangial conceptacle showing escaping spermatia and ring of cells (1) round conceptacle neck which produces the spout (2).

As mentioned previously, the development and structure of the conceptacle is essentially similar for carpogonial/carposporangial, tetra- and bisporangial conceptacles. Spermatangial conceptacles have basically the same process of development but the mature conceptacles are simple, flask-like structures (Fig. 12H) usually immersed in the thallus at the edge of carpogonial conceptacles. The ostiole filaments are reduced to a ring of cells round the neck of the conceptacle and produce a hyaline spout through which the spermatia are released. In one species, *P. concollum*, a similar spout develops on top of some of the collar-like ostioles of the other conceptacle types.

Gametangia and the carposporangial phase

Gametangial crusts are almost always monoecious, with spermatangial conceptacles occurring adjacent to the carpogonial/carposporangial conceptacles. Under certain environmental conditions, however, carpogonial conceptacles may fail to develop and crusts bearing only spermatangial conceptacles occur; this has been seen, for example, in *Fosliella farinosa* collected from the shore in winter (Chamberlain, 1977*b*).

Spermatangial structure shows little variation among *Fosliella* and *Pneophyllum* species. Fertile initials (spermatangial mother cells) develop from the floor of the conceptacle only; they produce elongated processes (Fig. 12H), usually from two sites on each initial, and these are eventually cut off and released into the chamber of the conceptacle. Here they round off to form more or less oval spermatia.

The oögonium is borne on a procarp (Figs 12C; 13) which comprises a supporting cell bearing one or two carpogonial branches and often a sterile filament. Each carpogonial branch consists of a hypogynous cell and a carpogonium, which has a swollen basal portion containing the oögonium and an extended, tube-like, upper portion, the trichogyne, through which the spermatium enters to fertilise the oögonium. In all species of *Pneophyllum* fertile procarps, bearing one or two carpogonial branches, occur in the centre of the fertile disc, while simpler structures without carpogonia occur at the periphery (Fig. 12C); a similar gradation has been noted in most coralline algae (Lebednik, 1977). In *Fosliella* only a single carpogonium has been observed on each procarp in the present investigation, and this is corroborated by the observations of Balakrishnan (1947, as *Melobesia farinosa*) and also appears to be the case in the illustrations of *F. farinosa* in Gordon *et al.* (1976); on the other hand, Masaki & Tokida (1960, pl. VII, Fig. 2) show two carpogonia on some procarps of *F. farinosa* (as *Melobesia*). While further investigation is needed, it seems possible that the presence of two carpogonia in *Pneophyllum*, and one in most samples of *Fosliella,* is a character of generic significance. Suneson (1937) put

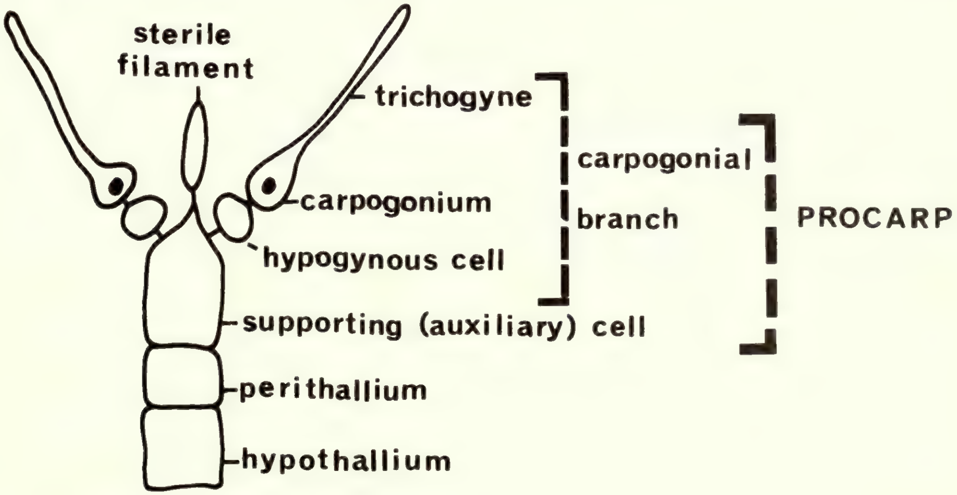


Fig. 13 An hypothetical coralline procarp.

forward the hypothesis that in the Corallinaceae procarps of 'primitive' taxa bear more carpogonia than those of 'advanced' types, which suggests, therefore, that *Fosliella* may represent a more 'advanced' evolutionary line than *Pneophyllum*.

As in all corallines, once a carpogonium has been fertilised the usual sequence of events leading to the formation of a fusion cell occurs. No evidence to prove the path taken by the zygotic nucleus in this process was uncovered in the present investigation, but Suneson (1937) figured a tube leading from the carpogonium to the auxiliary cell in *P. lejolisii* (as *Melobesia*). In *Pneophyllum* there seems to be no cellular connection between the fusion cell and subtending thallus cells which usually wither away; in British material of *Fosliella farinosa* (see p. 347) however, cell connections may appear between the fusion cell and the persistent subtending cells, and these were also observed by Balakrishnan (1947, as *Melobesia*). This is a further feature of possible significance. In the *Pneophyllum* species studied, the fusion cell varies from a thin, wide, pancake-like structure, closely appressed to the conceptacle floor (as in *P. concollum*) to a short, dumpy structure which is often situated high in the conceptacle cavity (as in *P. sargassi*). In all cases, gonimoblast filaments bearing terminal carposporangia develop from the periphery of the fusion cell (Figs 12E, F), and the remaining procarps in the centre of the fusion-cell surface (Fig. 12G) gradually disintegrate. Previously (Chamberlain, 1977*a*) it seemed that in British material of *P. limitatum*, gonimoblast filaments develop from the entire upper surface as well as the periphery of the fusion cell, as observed by Suneson (1937) in Swedish plants. Further examination has not confirmed this and although mature conceptacles are so packed with gonimoblast filaments and carposporangia that they occupy the whole area in surface view, almost all the gonimoblast filaments are initiated peripherally. However, on one occasion a filament appeared to be borne on the upper surface of the periphery of a fusion cell.

Tetrasporangia and bisporangia

Tetrasporangia develop peripherally in all species (e.g. Fig. 14A). In most taxa sterile paraphyses have not been seen to develop among the sporangia, although remnants of old perithallial cells are often observed in the centre of the conceptacle. In *P. concollum* (*q.v.*), however, a conspicuous central columella develops. All tetrasporangia develop in a manner characteristic of the Mastophoroideae (Chamberlain, 1982). The tetrasporangial initial (Fig. 15A) enlarges from the conceptacle floor, divides horizontally into a lower, stalk cell, which persists and develops no further, and an upper cell which enlarges to form the tetrasporangium. In species such as *P. lejolisii*, the young tetrasporangia are pigmented and the sporangium remains farctate throughout development, with the eventual septa appearing as thin lines in side view. In other species such as *P. rosanoffii* and *Fosliella farinosa* (*q.v.*), the young sporangium is pale, thread-like, deeply invaginated, and enclosed in a loose, sac-like casing; the sporangia expand in this pale, invaginated form, and only in the final stages of development do they become pigmented and farctate.

Variations in the structure (Fig. 14B) and development of bisporangia resemble those of the tetrasporangium in the same taxon; bisporangial development in *F. farinosa*, for example, is described (Chamberlain 1977*b*). Bisporangial plants with binucleate bispores are known in both genera (e.g. in *F. farinosa* – Balakrishnan, 1947, as *Melobesia*) but plants with uninucleate (and presumably diploid) bisporangia are probably more common, especially in colder climates (see Bauch, 1937, and Suneson, 1950).

Life history

A self-perpetuating, bisporangial life history (Fig. 15C) has been shown in plants of *F. farinosa* (Chamberlain, 1977*b*) with uninucleate bispores. In the present study (Chamberlain, 1982) the morphological sequences of a *Polysiphonia*-type (Fig. 15B) life history (Dixon, 1973) have been fully established for *Pneophyllum lobescens* and *P. myriocarpum*, and partly for *P. plurivalidum* and *Fosliella farinosa*, while a self-perpetuating bisporangial life history is demonstrated in *Pneophyllum zonale, P. lobescens,* and *P. plurivalidum.*

Summary

The most fundamental and consistent character separating *Fosliella* and *Pneophyllum* is the presence of a four-celled central element to the germination disc in *Fosliella,* and an eight-celled central element in *Pneophyllum.* In practice, however, this feature is not usually observable, and the two genera are, therefore, most easily distinguished by the presence of terminal hypothallial trichocytes divided by a tangential wall in *Fosliella,* as opposed to intercalary hypothallial trichocytes divided by a radial wall in *Pneophyllum.* However, abnormal, very large terminal trichocytes (at least twice the length of crust cells), lacking a dividing wall, have been observed in *Pneophyllum,* although intercalary trichocytes are so far unknown in *Fosliella.*

Two further features which may possibly prove of significance in distinguishing the genera are: (*a*) the presence of two carpogonia on at least some of the procarps of all species of

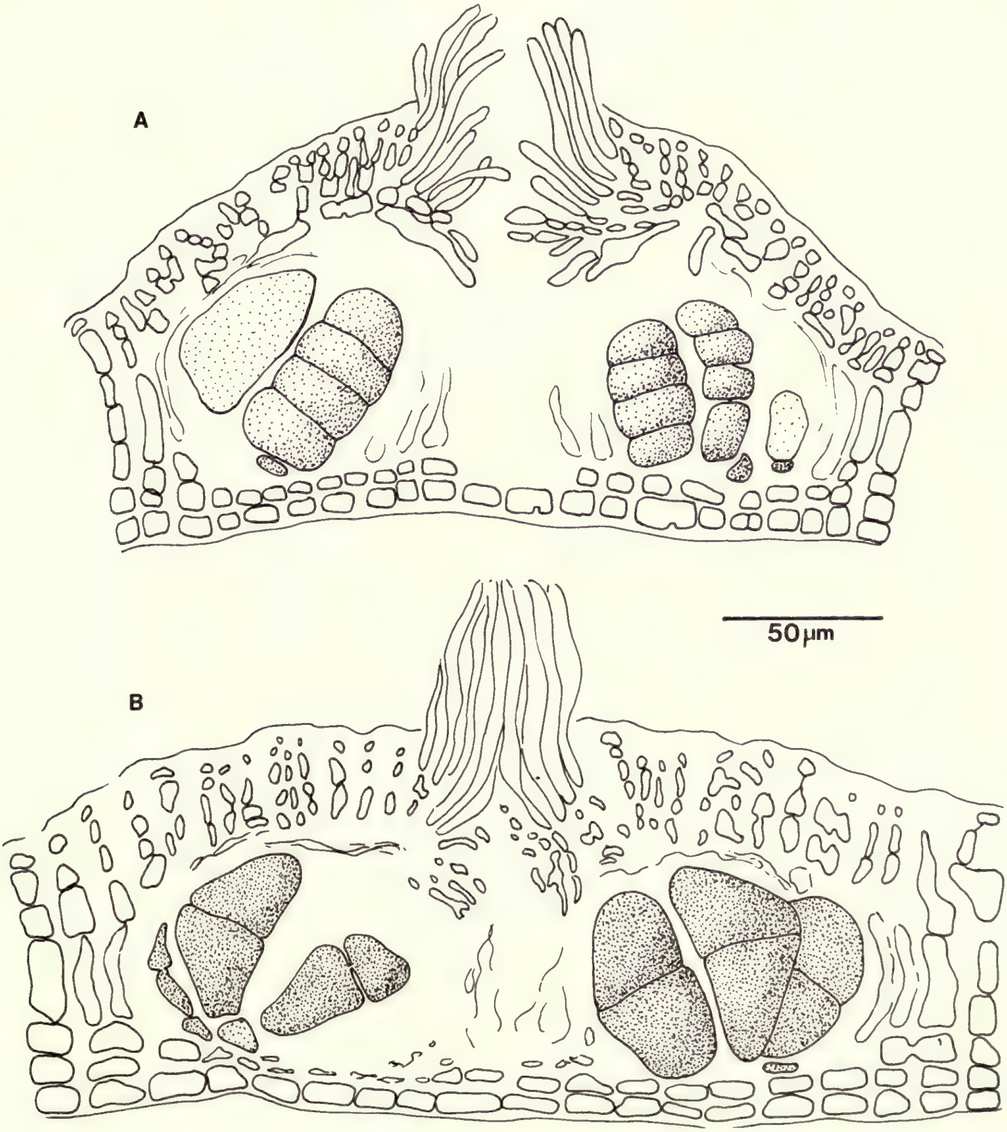


Fig. 14 The structure of tetrasporangial and bisporangial conceptacles in *Pneophyllum zonale.* A, Vertical section of tetrasporangial conceptacle. B, Vertical section of bisporangial conceptacle.

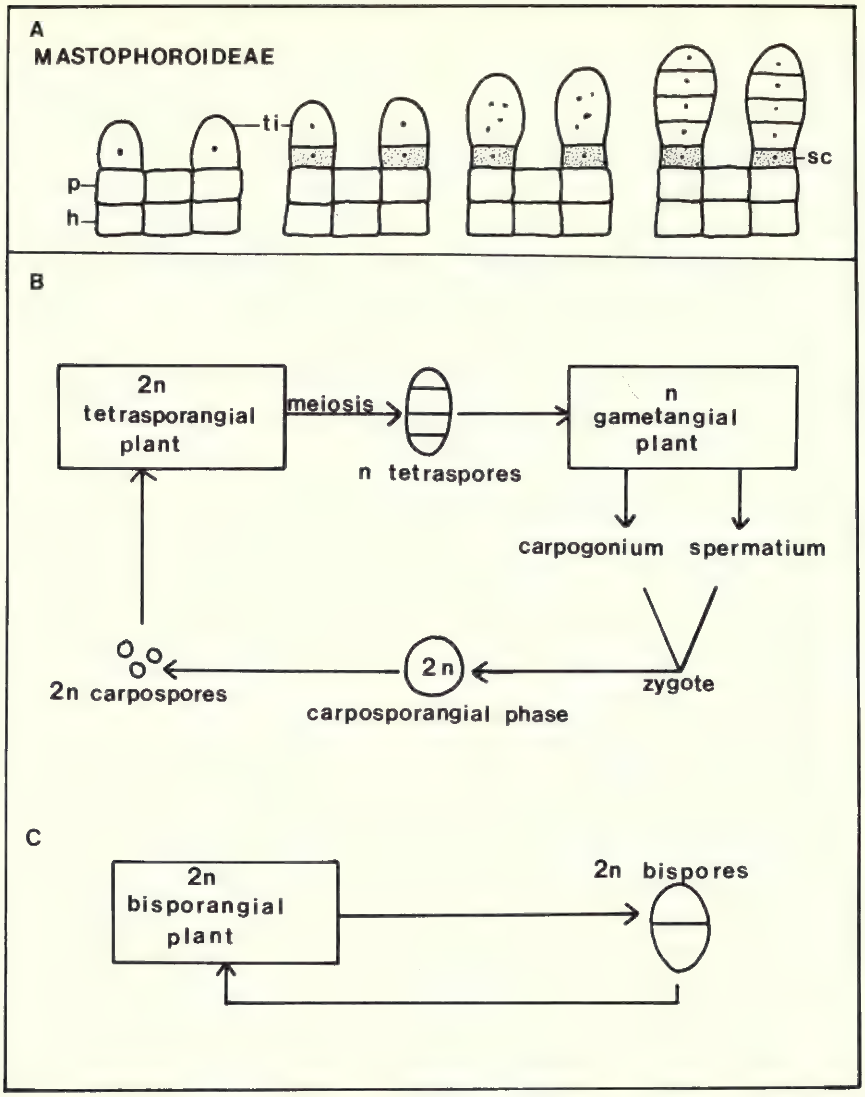

A
MASTOPHOROIDEAE
ti
p
h
sc
B
2n tetrasporangial plant
meiosis
n tetraspores
n gametangial plant
carpogonium
spermatium
zygote
2n
carposporangial phase
2n carpospores
C
2n bisporangial plant
2n bispores

Fig. 15 Tetrasporangial development and life-history phases in *Fosliella* and *Pneophyllum*. A, Tetrasporangial development: p = perithallial cell, h = hypothallial cell, ti = tetrasporangial initial, sc = stalk cell. B, *Polysiphonia*-type life history. C, Bisporangial life history.

Pneophyllum, as opposed to the single carpogonium almost always observed in *Fosliella*; and (*b*) the presence of a cellular connection between the fusion cell and subtending conceptacle floor cells in *Fosliella*, but not in *Pneophyllum*. A detailed survey of these features throughout the genera would be valuable.

The classification of the Corallinaceae

The Corallinaceae belong to the order Cryptonemiales, an order which Kylin (1956) characterised as having auxiliary cells which are present before fertilisation, and which occur as accessory filaments either adjacent to, or remote from, the carpogonium. Traditionally the members of the Corallinaceae have been divided into two groups, containing the crustose and the geniculate forms respectively, in a scheme of classification initiated by Areschoug (1852). More recently,

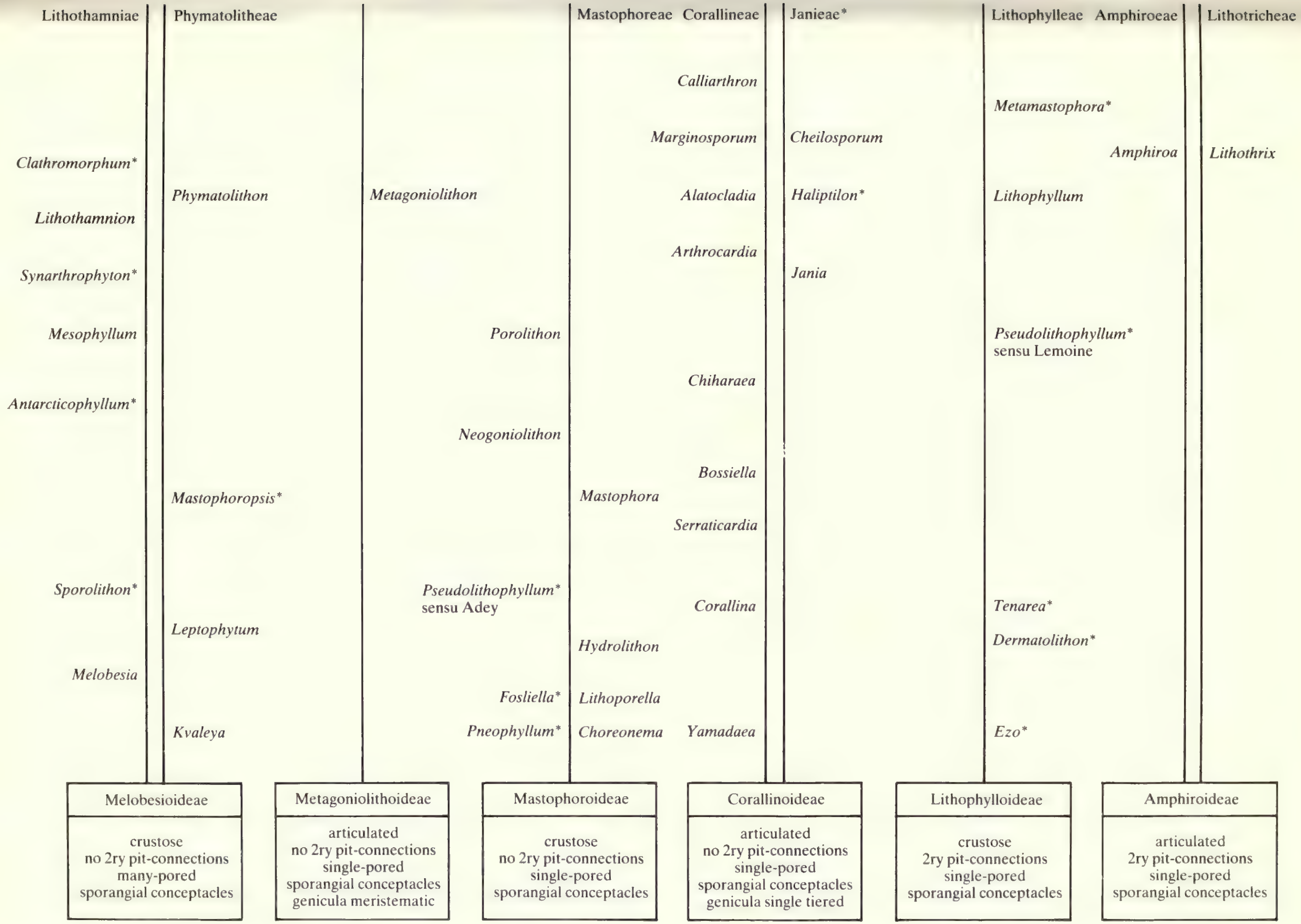

Lithothamniae
Phymatolitheae
Mastophoreae
Corallineae
Janieae*
Lithophylleae
Amphiroeae
Lithotricheae
*Clathromorphum**
Lithothamnion
*Synarthrophyton**
Mesophyllum
*Antarcticophyllum**
*Sporolithon**
Melobesia
Phymatolithon
*Mastophoropsis**
Leptophytum
Kvaleya
Metagoniolithon
Porolithon
Neogoniolithon
*Pseudolithophyllum**
sensu Adey
*Fosliella**
*Pneophyllum**
Mastophora
Hydrolithon
Lithoporella
Choreonema
Calliarthron
Marginosporum
Alatocladia
Arthrocardia
Chiharaea
Bossiella
Serraticardia
Corallina
Yamadaea
Cheilosporum
*Haliptilon**
Jania
*Metamastophora**
Lithophyllum
*Pseudolithophyllum**
sensu Lemoine
*Tenarea**
*Dermatolithon**
*Ezo**
Amphiroa
Lithothrix
Melobesioideae
crustose
no 2ry pit-connections
many-pored
sporangial conceptacles
Metagoniolithoideae
articulated
no 2ry pit-connections
single-pored
sporangial conceptacles
genicula meristematic
Mastophoroideae
crustose
no 2ry pit-connections
single-pored
sporangial conceptacles
Corallinoideae
articulated
no 2ry pit-connections
single-pored
sporangial conceptacles
genicula single tiered
Lithophylloideae
crustose
2ry pit-connections
single-pored
sporangial conceptacles
Amphiroideae
articulated
2ry pit-connections
single-pored
sporangial conceptacles

Fig. 16 The classification of the family Corallinaceae Lamouroux after Adey & Johansen (1972). Entries marked by an asterisk have been added by the present author on the basis of information published since 1972 and detailed in Chamberlain (1982).

however, it has been appreciated that other characters are of possibly greater taxonomic importance, and the characters now considered to be phylogenetically significant are the number of pores in the roof of the sporangial conceptacle and the type of secondary lateral anastomosis present (i.e. cell fusion or secondary pit connection).

Two principal schemes of suprageneric classification have emerged in recent years which have many points in common, but differ radically in that the presence or absence of a geniculum is proposed as a primary distinguishing character in one scheme, whereas in the other it assumes only secondary importance. The first scheme has been established by Johansen (1969, 1976, 1981), Adey & Johansen (1972) and Adey & Macintyre (1973), and in this scheme (Fig. 16) the family is divided into six subfamilies according to the possession of three characters, viz. conceptacle roof type, secondary synapse type, and presence or absence of genicula. Cabioch (1971*a*; 1972), on the other hand, considers that the conceptacle roof type and secondary synapse type are the fundamental characters, and classifies the geniculate forms in subfamilies together with the crustose forms with which they share these characters. I followed Cabioch's scheme in a previous publication (Chamberlain, 1978) and still consider this to present an evolutionarily more acceptable hypothesis than Adey & Johansen's scheme. Nevertheless, I have for the present retained the Mastophoroideae in the latter sense since, as commented by K. A. Johnson (1977) 'this scheme of classification divides the family into recognisable and taxonomically functional subgroups'. At present, many authors consider that the Corallinaceae should be raised to ordinal rank and removed from the Cryptonemiales, since it has many characters unique to its members; until this new classification is proposed it is preferable to maintain the present grouping rather than suggest further modifications.

Taxonomy of *Fosliella* and *Pneophyllum*

Introduction

In the present section *Fosliella* and *Pneophyllum* are formally described on the basis of the evidence presented in this investigation. A guide to identification, generic and species keys, and descriptions of British Isles species are given.

The organisation of species descriptions

Introduction

The structure and development of *Fosliella* and *Pneophyllum* are described under "Coralline structure" and the following species descriptions are based on the vegetative and reproductive characters discussed there. The format adopted for species descriptions is based on that recommended for the *Biological flora of British marine algae* (Burrows, 1959).

Taxonomic categories and nomenclature

As Dixon (1970, 1973) and Boney (1978) have remarked, the taxonomy of red algae is still at a very primitive stage because information about the organisms is still largely inadequate. Difficulties also arise because the theory, practice and rules of plant taxonomy have grown up around the study of angiosperms: they are not necessarily directly applicable to the algae, in which the simplicity of the thallus and effects of the aqueous environment upon it, are very different. Nevertheless, the same taxonomic categories are in use for both groups and are applied in the present investigation. Suprageneric (p. 330) and generic (pp. 319, 329) categories have been considered earlier; the remaining categories used in the present taxa are the species and the form.

As Davis & Heywood (1963) remark, the **species** is both the basic and the most controversial taxonomic category. It is assumed to have a genetic basis, but in practice recognition depends mainly on the assessment of phenetic characters. This is certainly true of the coralline algae where very little is known about chromosome numbers and characters. In the present taxa, therefore, the designation of species is based mainly on vegetative and reproductive characters in conjunction with some understanding of the way in which these characters are modified in response to changes in local and geographical factors of the environment. As is usually the case (cf. During, 1977) some species appear to be stable and are easily circumscribed (e.g. *P. rosanoffii* and *P. limitatum*); others, however, show great plasticity (e.g. *P. confervicolum*).

The final category, the **forma**, should preferably also have a genetic basis (During, 1977) and, strictly speaking, should probably not be used to distinguish the creeping forms *P. confervicolum* f. *minutulum* and *Fosliella farinosa* f. *callithamnioides*. It is, however, valuable to be able to refer to these characteristic growth forms by name and, as forma has been used in this sense by previous authors (e.g. Foslie, 1908*a* and Suneson, 1943), its use is continued here.

The species descriptions begin with a discussion of the historical knowledge of the taxon. The basionym is given for each species and the synonymy and references are divided into four sections: (1) Nomenclatural, or obligate, synonyms based on the same type as the basionym (Stafleu *et al.*, 1978: Article 14.2). (2) References: printed records which, in my opinion, are referable to the taxon concerned (they may *either* have been given the name of the basionym, or a nomenclatural synonym; *or* be a taxonomic synonym; *or* have been mis-attributed to a different taxon). (3) Specimens: herbarium specimens which I have examined and which are referable to the taxon concerned. (4) Excluded records: printed records and herbarium specimens which, in my opinion, have been wrongly attributed to the taxon concerned.

Diagnosis and description

The diagnosis and description are drawn up along the lines indicated by Stearn (1973: 147–154, 165–167) and refer to British material unless otherwise indicated.

Measurements

Because rather few characters are available for species recognition in simple crustose corallines, much reliance has previously been placed on the comparison of dimensions. While it has become clear from culture experiments (Chamberlain, 1982) and sequential field observations that dimensions must be treated with some caution because they are subject to environmental modification, nevertheless those based on material growing under favourable conditions are a useful character. Measurements based mainly on material collected in the present investigation are tabulated for each species. Where appropriate the dimensions are compared with other published figures. A minimum, mean, and maximum value is given for each dimension unless it was not possible to obtain sufficient material. The number of measurements taken depends on the character concerned; for crust cells in surface view, for example, a block of about 20 cells behind (but not including) the first meristem is measured from about five crusts, while for conceptacles, 5–20 are measured. Cell measurements are made between middle lamellae (Figs 17B, C) which is probably comparable with most published descriptions, although Adey & Adey (1973) measure cell lumina. Crust thickness and diameter are imprecise values, but are usually given by Lemoine and Foslie in their various publications and are included here for comparison; crust diameters are measured on mature crusts and thickness measurements are made beside conceptacles (Fig. 17C). Conceptacle diameters are given as both VS internal diameter (Fig. 17C) and *internal* surface diameter based on *decalcified* whole mounts. Unfortunately, many published descriptions fail to specify how conceptacle diameter is measured but the figure often alludes to the *external* diameter as seen in *calcified* material. The approximate position of such a measurement is shown at '16' on Figure 17C; as it is a very imprecise measurement it has not been used in the present study but can be assumed to be considerably larger than the internal diameters given.

Vegetative characters

Since S.E.M. techniques have become available, it is possible to make cell measurements on the calcified crust surface. Garbary (1978) studied a range of complex and simple crustose corallines by this means: he noted qualitative differences among genera and species and also made a statistical study of relative sizes of crust cells and epithallial concavities. However, since all

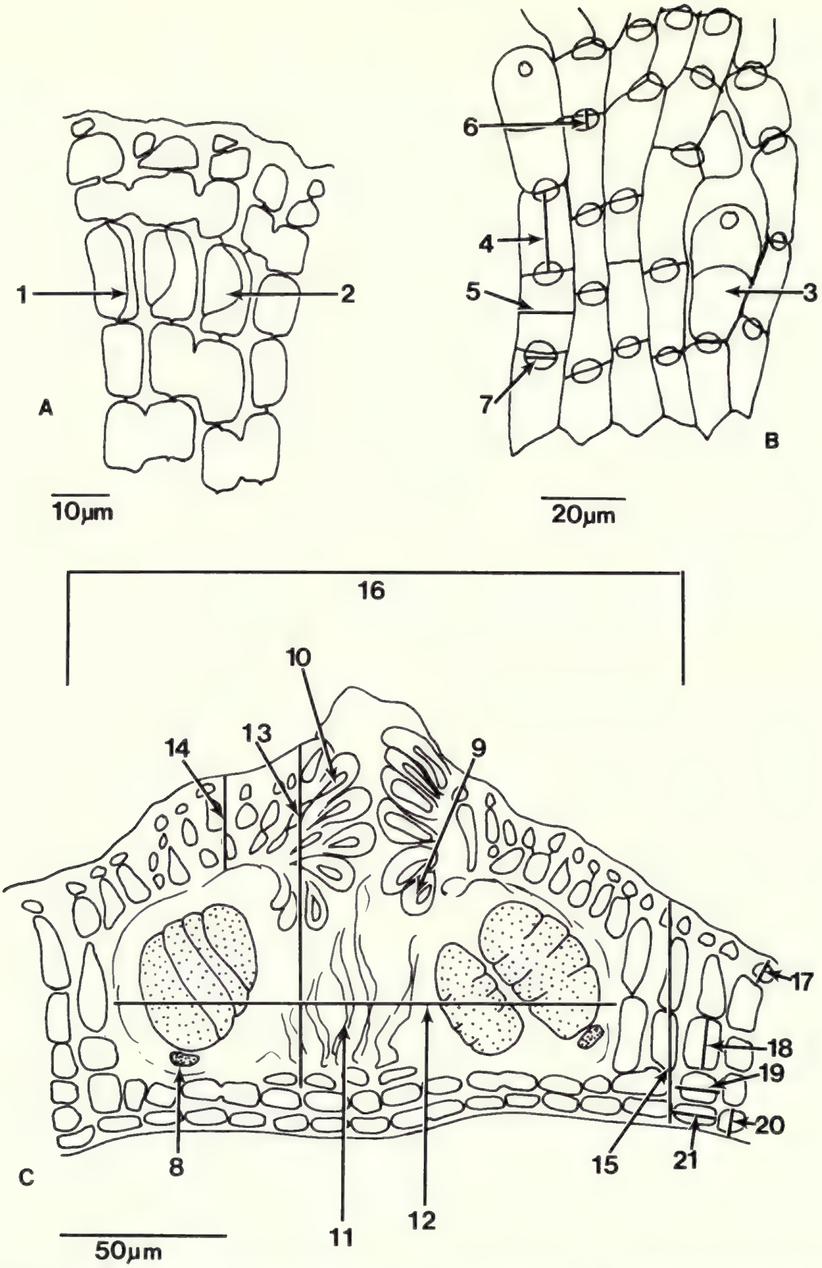


Fig. 17 Features of *Pneophyllum* and *Fosliella*. A, Surface view of decalcified crust of *Pneophyllum rosanoffii* focused to show cell lumina and cell fusions, intercalary intrafilament trichocyte (1), and intercalary branch cell trichocyte (2). B, Surface view of calcified crust of *Fosliella farinosa* focused to show positions of middle lamellae, terminal trichocyte (3), and positions at which crust cell length (4) and width (5) and epithallial cell length (6) and width (7) measurements are made. C, Vertical section of tetrasporangial conceptacle of *Pneophyllum concollum* showing stalk cell (8), downward ostiolar filaments (9), upward ostiolar filaments (10), central sterile 'paraphyses' (11), and positions at which the following measurements are made: conceptacle internal diameter (12) and height (13), roof height (14), crust depth (15), conceptacle external diameter (16), epithallial cell height (17), perithallial cell height (18) and width (19), and hypothallial cell (VS) height (20) and width (21).

previous published records have been made on light microscope preparations, and as this technique is much more generally available, these dimensions are used here. Qualitative features seen under the S.E.M. are, however, important and are noted in the description.

The presence or absence of a perithallium and its depth, when present, are important characters, and the dimensions of perithallial and hypothallial cells in vertical section may be distinctive. It is important, however, to recognise that many crusts are almost entirely composed of conceptacles; a section through these invariably cuts tangentially through conceptacle walls, as well as chambers, and this may give the appearance of a deep perithallium (e.g. in *Pneophyllum lejolisii* cf. Lemoine, 1911). While a perithallium is most clearly seen in vertical section, it is often possible to detect its presence by focusing up and down on whole mounts.

Hypothallial trichocytes occur in many species; in *Fosliella* they are always terminal (Fig. 17B) and the presence of 'normal'-sized, terminal trichocytes which are less than twice the length of crust cells (excluding the length of the basal cell) is sufficient to determine the genus. When present in *Pneophyllum* (see p. 323) trichocytes are 'normally' intercalary and may occur either at a filament branch (branch cell type, Fig. 17A) or in unbranched filament cells (intrafilament type, Fig. 17A). In *Pneophyllum* exceptionally large and irregular terminal trichocytes (at least twice the length of crust cells) occasionally occur (Chamberlain, 1982) but it should not be difficult to distinguish these from the 'normal' ones of *Fosliella farinosa*.

In general, colour is not a useful distinguishing character because it can vary so much with environmental conditions and is often entirely lost in preserved material. An attempt has been made, however, to match crust colours with Ridgway's (1912) code, and these colours are included in the vegetative dimension tables of some species.

Reproductive characters

It is principally the qualitative and quantitative features of conceptacle construction that distinguish the species. The most apparent feature, apart from diameter and height (Fig. 17C), is the nature of the ostiole and the filaments which surround it (Fig. 17C). These filaments may be almost undeveloped (e.g. *Fosliella farinosa, Pneophyllum lejolisii*), form a dome of wedge-shaped cells (e.g. *P. lobescens, P. plurivalidum*), be extended into either an elaborate funnel shape (*P. limitatum*), or form various types of tentacle-like structure (e.g. *P. rosanoffii, P. zonale*). This feature may be observed both in decalcified preparations under the light microscope and calcified material under the S.E.M.

As discussed on p. 324, as a conceptacle develops, the roof is formed from new filaments initiated from perithallial cells. Under the S.E.M. it can be seen that three types of conceptacle roof may be formed: (*a*) Uniform: in which the original thallus surface remains intact (e.g. *P. lejolisii, P. rosanoffii*). (*b*) Irregular: in which the original thallus surface sloughs off irregularly to reveal the rounded roof cells below (e.g. *P. zonale*). (*c*) Zonal: in which the original thallus surface disappears from the centre of the conceptacle roof and is restricted to a ring round the base (e.g. *P. sargassi, Fosliella farinosa*). While this character can only be seen under the S.E.M., deductions about it may be made by focusing up and down on whole mounts and by observing the upper surface of the roof in vertical section. In all species young conceptacles have a uniform surface.

The ostiole and roof characters discussed above apply to all conceptacle types except the spermatangial, which is usually a simple structure immersed in the thallus beside the carpogonial conceptacle, the ostiole is prolonged into a spout although this is not always easy to observe.

The reproductive bodies show relatively little variation between species but some features may be of assistance in identification, e.g. the number of carposporangial filaments (best seen in young, decalcified whole mounts) and the size and shape of the fusion cell which, for example, is wide and very shallow in *Pneophyllum concollum* and narrow and deep in *P. sargassi*. In tetrasporangial and bisporangial conceptacles the number and size of the sporangia may be useful and two further features show variation among the species, these are:

A. In some species (e.g. *P. rosanoffii* and *Fosliella farinosa*) the sporangia are initiated as thread-like, pale structures, which are deeply invaginated and only become farctate and densely pigmented on maturity, when they finally divide into two or four spores. In other species the sporangia are farctate and pigmented throughout development.

B. There is variation in the amount of development of sterile cells ('paraphyses', 'columella') in the centre of the conceptacle floor (Fig. 17C); *P. concollum* has particularly pronounced central paraphyses which may swell into balloon-like structures.

Culture methods for separating epilithic species of Pneophyllum

The morphology of epilithic species of *Pneophyllum* was investigated principally on crusts grown in the laboratory (Chamberlain, 1982). Epilithic simple crusts were particularly difficult to investigate because they fragmented easily when removed from the substratum and generally grew in very mixed communities. The cultures were initiated from crusts growing on a piece of glass collected from the mouth of the River Yealm, south Devon, from which were grown eight crust types belonging to four species of *Pneophyllum* as follows:

Pneophyllum lobescens – bisporangial, gametangial, tetrasporangial
Pneophyllum myriocarpum – gametangial, tetrasporangial
Pneophyllum plurivalidum – bisporangial, gametangial
Pneophyllum zonale – bisporangial.

The crusts were separated out and cultured as described on page 296 and life history and morphological studies were made on these crusts. A *Polysiphonia*-type life history was established for *Pneophyllum lobescens* and *P. plurivalidum* and a self-perpetuating bisporangial life history for *P. lobescens, P. plurivalidum,* and *P. zonale.* Morphological studies showed that crust cell size and shape varied considerably during the year, generally the species were easily distinguished from each other between about May and October, but resembled each other much more closely at other times; Bressan *et al.* (1977) made similar observations on Adriatic species. It was also found that the crusts generally reproduced abundantly and produced fertile spores from about May to October, but reproduced more slowly at other times and sometimes produced conceptacles lacking, or with non-fertile, spores.

Distribution and other features

A knowledge of distribution, phenology, form range, and substratum preference is considered to be of importance in the systematics of the present taxa. The localities at which most of the collections were made are shown in Figure 18, while a list of plants and other substrata with their most frequently occurring crusts is given below. Published records of British Isles material are given in Table 5, and a detailed list of specimens seen in herbaria is given in Chamberlain (1982).

Summary

Species identification is based principally on the following features: (*a*) Crust cell dimensions, (*b*) Presence or absence of perithallial filaments and length when present, (*c*) Conceptacle size and shape, (*d*) Conceptacle roof and ostiole structure, (*e*) Number, size and development of tetra- and bisporangia, (*f*) Degree of development of sterile 'paraphyses' in tetra- and bisporangial conceptacles.

Substrata

As an aid to identification, the following list of substrata with their most frequently occurring crust species has been drawn up:

Zostera marina L.
    Pneophyllum lejolisii, P. limitatum (small amounts), *P. rosanoffii* (increasingly common towards western England and Ireland); *Fosliella farinosa* (occasional, but dominant locally, e.g. The Fleet, Dorset)
Chondrus crispus Stackh. in exposed places
    Melobesia membranacea; Dermatolithon pustulatum
Chondrus crispus elsewhere
    Pneophyllum limitatum, P. microsporum (especially winter), *P. zonale* (occasionally); *Fosliella farinosa*; *Melobesia membranacea*

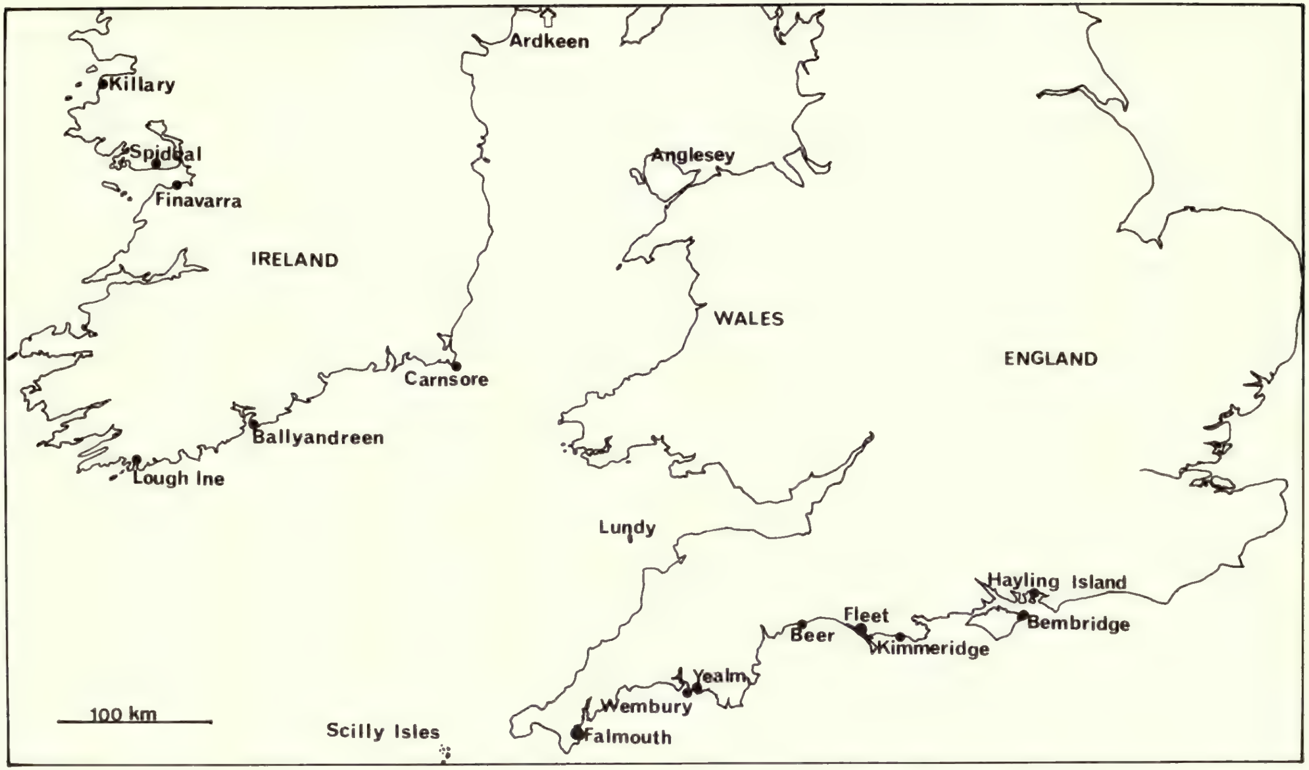

Ardkeen
Killary
Spiddal
Finavarra
IRELAND
Carnsore
Ballyandreen
Lough Ine
Anglesey
WALES
ENGLAND
Lundy
Hayling Island
Bembridge
Fleet
Beer
Kimmeridge
Yealm
Wembury
Falmouth
Scilly Isles
100 km

Fig. 18 The southern part of the British Isles showing the localities at which the principal collections of simple crustose corallines were made (Ardkeen is about 20 km north of the map).

Corallina officinalis L.
  Dermatolithon corallinae; *Mesophyllum lichenoides*
Furcellaria lumbricalis (Huds.) Lamouroux
  Melobesia membranacea (very commonly); *Pneophyllum microsporum*; *Dermatolithon* spp.
Gastroclonium ovatum (Huds.) Papenf.
  Pneophyllum concollum (Devon and Ireland); *Melobesia membranacea*
Gigartina stellata (Stackh.) Batters in exposed places
  Melobesia membranacea; *Dermatolithon pustulatum*
Gracilaria verrucosa (Huds.) Papenf.
  Pneophyllum concollum (Devon); *Melobesia membranacea*; *Dermatolithon* spp.
Halopitys incurvus (Huds.) Batters
  Melobesia membranacea (very commonly); *Pneophyllum rosanoffii, P. sargassi*
Jania rubens (L.) Lamouroux
  Pneophyllum confervicolum; *Choreonema thuretii*
Laurencia pinnatifida (Huds.) Lamouroux
  Pneophyllum confervicolum, P. microsporum, P. limitatum; *Melobesia membranacea*; *Dermatolithon* spp.
Palmaria palmata (L.) Kuntze
  Pneophyllum limitatum (especially autumn), *P. concollum* (increasingly towards the west), *P. confervicolum, P. rosanoffii* (at Beer); *Fosliella farinosa* (especially autumn); *Melobesia membranacea*
Phyllophora crispa (Huds.) P. Dixon and *P. pseudoceranoides* (S. Gmelin) Newr. & A. Taylor
  Melobesia membranacea; *Dermatolithon pustulatum*
Polysiphonia elongata (Huds.) Sprengel
  Pneophyllum concollum (Ireland), *P. limitatum*; *Fosliella farinosa*
Cystoseira nodicaulis (With.) M. Roberts
  Fosliella farinosa (especially on tophules); *Dermatolithon* spp.
Dictyota dichotoma (Huds.) Lamouroux
  Pneophyllum limitatum, P. confervicolum
Fucus serratus L.
  Pneophyllum limitatum (especially autumn), *P. confervicolum*; *Fosliella farinosa* (especially autumn)
Laminaria spp.
  Holdfasts: *Melobesia membranacea* and *Dermatolithon pustulatum* f. *laminariae*
  Fronds: *Pneophyllum limitatum* (especially autumn), *P. confervicolum*; *Fosliella farinosa* (especially autumn)
Sargassum muticum (Yendo) Fensholt
  Pneophyllum limitatum; *Fosliella farinosa*
Cladophora rupestris (L.) Kütz.
  Pneophyllum confervicolum; *Melobesia membranacea*; *Dermatolithon litorale*
Rissoid shells
  Pneophyllum myriocarpum, P. zonale
Glass, stones, etc.
  Pneophyllum zonale, P. myriocarpum, P. lobescens, P. plurivalidum; *Fosliella farinosa*; *Melobesia membranacea*

Generic key

Key to the genera of simple crustose Corallinaceae in the British Isles:

1 Roof of tetrasporangial conceptacle with many pores .... **Melobesia**
– Roof of tetra- or bisporangial conceptacle with a single pore 2

2(1) Trichocytes terminal .... **Fosliella**
– Trichocytes intercalary or absent 3

3(2) Hypothallial cells (in VS) square or wider than high .... **Pneophyllum**
– Hypothallial cells (in VS) vertically elongated, often curved .... **Dermatolithon**

Table 5 Published records of *Fosliella* and *Pneophyllum* in the British Isles.

[!] = records which have been checked against herbarium specimens
? = records which are dubious

South and south-West England (Dover to Severn Estuary, Scilly Isles, Lundy)
Fosliella farinosa
Anon., 1952: 45 (as *Melobesia*); Batters, 1902: 96 (as *Melobesia*) [BM!]; Chamberlain, 1977*b* [BM!]; Irvine *et al.*, 1972: 132 (as *Melobesia*); Russell, 1968: 581 (as *Melobesia*); Price *et al.*, 1981: 17 [BM!].
Pneophyllum lejolisii
Anon., 1952: 45 (as *Melobesia*); Batters, 1902: 96 (as *Melobesia*) [BM!]; Chamberlain, 1977*a*: 73 (as *Fosliella*) [BM!]; Russell, 1968: 581 (as *Melobesia*); Tellam, 1884: 339 (as *Melobesia*) [BM, Royal Cornwall Institute!].
Pneophyllum limitatum
Batters, 1902: 96 (as *Melobesia zonalis* incl. *M. myriocarpa*) [BM!]; Chamberlain, 1977*b*: 69 (as *Fosliella*) [BM!].
Pneophyllum confervicolum
Batters, 1892: 59 (as *Melobesia callithamnioides* on *Ulva lactuca,* good description but no specimen seen); Batters, 1902: 96 (as *Melobesia zonalis* incl. *M. myriocarpa* and as *M. callithamnioides*) [BM!]; Burrows, 1964: 365 (as *Melobesia*); Price *et al.*, 1981: 18 (as *Fosliella minutula*) [!].
Pneophyllum myriocarpum
Batters, 1902: 96 (as *Melobesia lejolisii*) [BM!].
Pneophyllum lobescens
Batters, 1902: 96 (as *Melobesia zonalis*) [BM!].
Pneophyllum zonale
Anon., 1952: 45 (as *Melobesia*): Adey & Adey, 1973: 397 (as *Fosliella tenuis*).

Channel Islands
Fosliella farinosa
Dixon, 1961: 76 (as *Melobesia*).
Pneophyllum lejolisii
Marquand, 1895: 371 (as *Melobesia*).
Pneophyllum confervicolum
Dixon, 1961: 76 (as *Melobesia minutula*).

Ireland (Further summaries are given in Cullinane, 1973, and Guiry, 1978)
Fosliella farinosa
Batters, 1902: 96 (as *Melobesia*); de Valéra *et al.*, 1979: 263; Foslie, 1905*a*: 69 (as *Melobesia farinosa* f. *borealis*) [TRH!]; Goss-Custard *et al.*, 1979: 33 [GLAS!]; Guiry, 1978: 140; Harvey, 1849: 109 (as *Melobesia*) ?; Johnson & Hensman, 1899: 26 (as *Melobesia*); Lemoine, 1913: 140 (as *Melobesia farinosa* on *Zostera,* as *M. zonalis* on shells) [BM-K!; DBN!].
Pneophyllum lejolisii
Batters, 1902: 96 (as *Melobesia*); de Valéra *et al.*, 1979: 263 (as *Fosliella*); Harvey, 1851: Pl. CCCXLVIIA (as *Melobesia membranacea*)?; Scannell, 1969: 193 (as *Melobesia farinosa*) [DBN!].
Pneophyllum rosanoffii
Johnson and Hensman, 1899: 27 (as *Melobesia lejolisii*).
Pneophyllum confervicolum
Adams, 1908: 51 (as *Melobesia confervicola*) ?; Allman *In* Harvey, 1848: pl. CLXVI (as *Lithocystis allmanni*) ?; de Valéra *et al.*, 1979: 263 (as *Fosliella minutula*); Johnson & Hensman, 1899: 26 (as *Melobesia confervoides*) ?; Lemoine, 1913: 1281 (included in *Epilithon membranaceum*) [DBN!]; Norton, 1970: 264 (as *Melobesia minutula* f. *lacunosa*).
Pneophyllum zonale
Adey & Adey, 1973: 397 (as *Fosliella tenuis*) ?

Wales and North West England (including Isle of Man)
Fosliella farinosa
Jones & Williams, 1966: 319 (as *Melobesia*); Knight & Parke, 1931: 102 (as *Melobesia*).
Pneophyllum lejolisii
Davey, 1943: 420 (as *Melobesia*).

Pneophyllum confervicolum
Baker *et al.*, 1957: 27 (as *Melobesia minutula*); Knight & Parke, 1931: 102 and 118 (as *Melobesia minutula*).
Pneophyllum zonale
Batters, 1902: 96 (as *Melobesia*); Jones & Williams, 1966: 311 (as *Melobesia*) ?; Adey & Adey, 1973: 397 (as *Fosliella tenuis*) ?

Scotland (including the islands)
Fosliella farinosa
Batters, 1891: 25 (as *Melobesia*); Traill, 1890: 338 (as *Melobesia*); Russell, 1962: 280 (as *Melobesia*).
Pneophyllum lejolisii
Batters, 1891: 25 and 1901: 29 (as *Melobesia membranacea*) [BM!, E!, GLAS!]; Sinclair, 1949: 173 (as *Melobesia farinosa*).
Pneophyllum confervicolum
Batters, 1891: 25 (as *Melobesia confervoides*) ?, 1902: 96 (as *Melobesia zonalis* including *Hapalidium confervoides*) ?; Sinclair, 1949: 173 (as *Lithothamnion membranaceum*) [E!].
Pneophyllum zonale
Batters, 1902: 96 (as *Melobesia*) ?; Adey & Adey, 1973: 397 (as *Fosliella tenuis*) *pro parte*.

Eastern England (Berwick-upon-Tweed to Dover)
Fosliella farinosa
Batters, 1890: 359 (as *Melobesia*).
Pneophyllum lejolisii
Batters, 1890: 358 (as *Melobesia*); Holmes exsiccata no. 265 (as *Melobesia*) [BM!].

I. *Fosliella*

Fosliella M. Howe *In* N. L. Britton & C. F. Millspaugh, *The Bahama flora*: 587 (1920).

TYPE SPECIES: *Fosliella farinosa* (Lamouroux) M. Howe (*Melobesia farinosa* Lamouroux, *Histoire des polypiers coralligènes flexibles vulgairement nommés zoophytes*: 315 (1816)).

HOLOTYPE: CN! Herb. Lamouroux, from the Mediterranean, growing on *Sargassum linifolium* (Fig. 19).

SYNONYMY: There are no nomenclatural synonyms of *Fosliella* but Foslie (1905*a*) included *Melobesia farinosa* in the subgenus *Eumelobesia* comprising species with a monostromatic thallus and heterocysts.

Foslie (1909) raised subgenus *Heteroderma*, of the genus *Melobesia*, to generic rank and mentioned that this left *Melobesia* sensu Foslie with the single species *M. farinosa*; he did not, however, make a formal description of the genus *Melobesia* in this sense.

DESCRIPTION: *Thallus* thin, calcified, crustose, mainly epiphytic on algae and marine angiosperms, occasionally epilithic on glass and stones or epizoic on shells; vegetative thallus composed of rectangular-celled hypothallial filaments and rounded epithallial cells; cell fusions frequent; hypothallial *trichocytes* terminal; propagules sometimes present in hotter climates. *Gametangial plants* usually monoecious, sometimes dioecious; carpogonial conceptacles raised, with central ostiole through which trichogynes protrude, fertile procarps bearing only one carpogonium; spermatangial conceptacles domed, prominent, ostiole prolonged into a spout. *Carposporangial conceptacles* domed, prominent, ostiole with very short filaments and sometimes a rosette on upper surface, roof surface irregular or zonal, frequently a ring of trichocytes round conceptacle base; fusion cell usually narrow and deep, often in open connection with subtending thallus cells. *Tetrasporangial plants* with single-pored conceptacles similar to carposporangial conceptacles, tetrasporangia borne peripherally on stalk cells, young tetrasporangia deeply invaginate, usually some development of central sterile cells. *Bisporangial plants* with uninucleate (presumably diploid) bispores known only in *F. farinosa* from northern Europe, conceptacles similar to tetrasporangial ones but larger, young bisporangia deeply invaginate, some development of central sterile cells; bisporangial plants with binucleate bispores occasionally reported (e.g. Balakrishnan, 1947), possibly these are incompletely divided tetrasporangia. *Spore germination disc* with central element of four cells each of which initiates hypothallial filaments from one surface only.

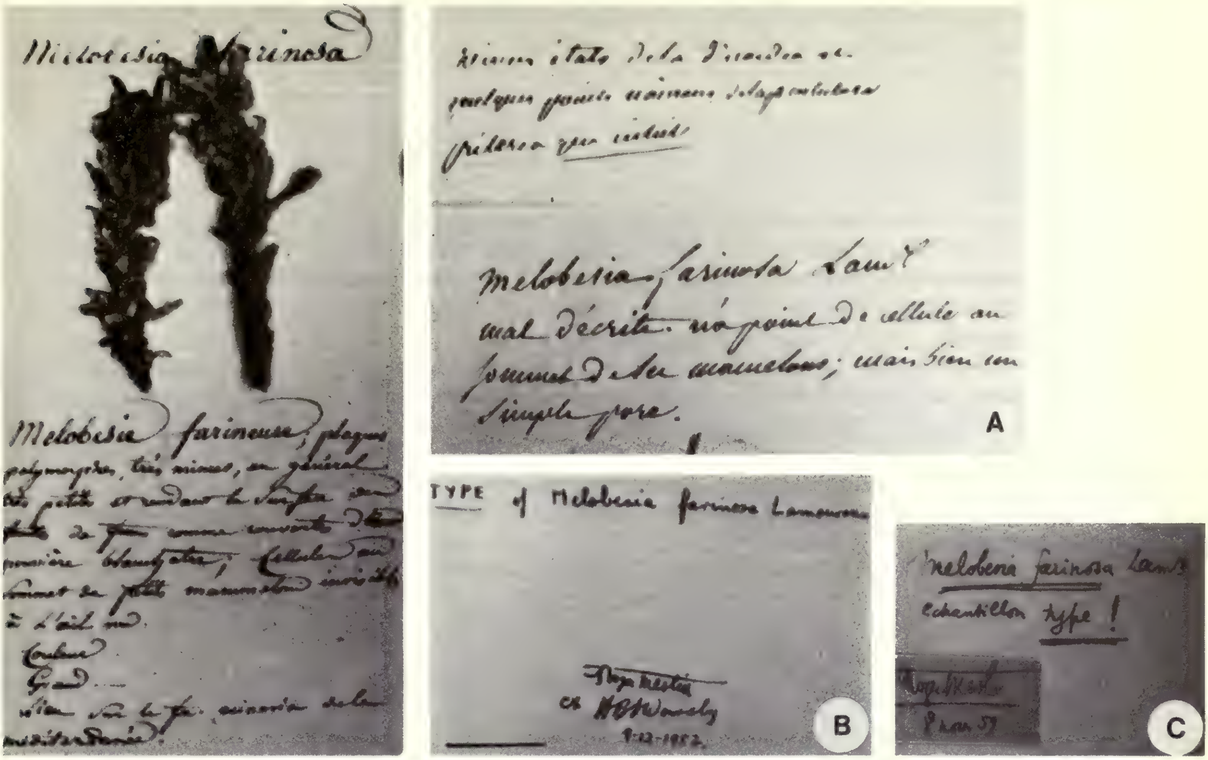

Melobesia farinosa Lamx
mal décrite. n'a point de cellule au
sommet de ses mamelons; mais bien un
simple pore.
A
TYPE of Melobesia farinosa Lamouroux
cx HBWomersley
9-12-1952
B
Melobesia farinosa Lamx
échantillon type!
C

Fig. 19 Type specimen of *Melobesia farinosa* Lamouroux from Herb. Lamouroux, Caen. The writing on the specimen is that of Lamouroux; the two labels A were written at different times by Rosanoff, label B was written by Womersley, and label C by Meslin. Scale = 15 mm.

HISTORICAL: The genus *Fosliella* was a new name proposed by Howe (1920) for *Melobesia* (subgen. *Eumelobesia* Foslie) sensu Foslie (1905*a* where a valid description is given on p. 96). *Fosliella* accommodates simple, crustose, coralline algae with single-pored sporangial conceptacles, with or without 'heterocysts' (i.e. trichocytes), and with perithallial filaments absent or up to nine cells deep. Howe designated *Fosliella farinosa* as the type, based on Lamouroux's (1816) species *Melobesia farinosa*. A new name had to be found for the genus *Melobesia* sensu Foslie (1905*a*) because Lamouroux (1812) had previously assigned another species, *Corallina membranacea* Esper (1806), to *Melobesia*, which had multi-pored sporangial conceptacles. The present emended description is, however, restricted to crusts without a vegetative perithallium, with terminal trichocytes and with a four-celled central element to the germination disc (see pp. 319–320).

SYSTEMATICS: Only three species of *Fosliella* have been described, these being *F. farinosa* (Lamouroux) M. Howe with two creeping forms, f. *callithamnioides* (Foslie) Y. Chamberlain and var. *chalicodictya* W. Taylor, *F. paschalis* (P. Lemoine) Setch. & N. Gardner, and *F. cruciata* Bressan in Bressan, Miniati-Radin & Smundin.

The essential features of the type species, *F. farinosa*, are described under that species and are seen in Lamouroux's type specimen which I examined at CN (Fig. 19). Material from the British Isles, French material described by Rosanoff (1866), and descriptions of material from India (Balakrishnan, 1947) and from Guam (Gordon *et al.*, 1976) all accord well with this concept, as do many collections from other areas. However, many specimens differ markedly in one or more ways. There is, for example, a form in which cells and conceptacles are about twice the size of normal material. I received such material, growing together with normal thalli, from the Canary

Islands (collected by W. F. Prud'homme van Reine) and have observed the same modification in herbaria (e.g. Titius, no. 855 from Spalato, identified by Rosanoff as '*Melob. farinosa* f. *macrocarpa*', in CN). This form corresponds in size with that recorded from Venezuela by Ganesan (1971).

The thin, vegetative thallus and abruptly-domed conceptacles are common to all descriptions, with the exception of the drawing by Masaki & Tokida (1960, Pl. VI, Fig. 7) which shows a tetrasporangial conceptacle immersed in a deep thallus. Terminal trichocytes are nearly always present except in winter and on material collected from deeper than about 5 m (Lemoine, 1923*a*; Chamberlain, 1977*b*), but sometimes crusts with and without trichocytes are found growing side by side (Lemoine, 1917; Ganesan, 1971). Lemoine (1917) also depicted differences in cell size and shape according to the host which is another factor to be taken into consideration regarding species variability.

The creeping forms, particularly *callithamnioides*, occur quite frequently, especially in warmer climes and I have observed f. *callithamnioides* in Ireland where the crusts may also show a transition from a uniform crust to a creeping filamentous form. The variety *chalicodictya* has been recorded from the Caribbean (Taylor, 1939) and the Mediterranean (Coppejans, 1976) while a further Mediterranean form (unnamed) was described by Boudouresque & Cinelli (1971) which bears a strong resemblance to the early germination filaments of *Amphiroa verruculosa* as depicted by Cabioch (1972, p. 147).

One further form, *Melobesia farinosa* f. *borealis*, was described by Foslie (1905*a*) from Ireland. This has proved to be the bisporangial phase of *F. farinosa* (Chamberlain, 1977*b*), which is the commonest phase of this species in the British Isles and has also been recorded from northern France (Lemoine, 1923a).

Fosliella paschalis was described from Easter Island by Lemoine (1923*b*, as *Melobesia*) as a small, greyish plant in which the thalli never superimposed; it had loosely coalescent hypothallial filaments, the conceptacles were smaller than in *F. farinosa* and were each borne on a mound of perithallial cells. Subsequent records of *F. paschalis* (e.g. Dawson, 1960; Masaki, 1968; Hollenberg, 1970) have confirmed the small conceptacle size and absence of superimposition of thalli, but none has mentioned the presence of perithallial mounds.

Vegetative propagules have been described in *Fosliella* – such structures occur very rarely in the Rhodophyta. Solms-Laubach (1881) described multicellular, triangular propagules growing on *F. farinosa* f. *callithamnioides* (as *Melobesia callithamnioides*) in the Mediterranean and the same type was described from f. *farinosa* by Coppejans (1978). Much simpler, unicellular, pear-shaped propagules were depicted by Hollenberg (1970) growing on *F. paschalis*.

F. cruciata occurs commonly in the Trieste area (Bressan *et al.*, 1977) and its distinctive characters were described as the germination disc pattern and the elongated terminal trichocytes, Bressan & Tomini (1983) suggest that it may be a polyploid species.

It seems certain that there are more *Fosliella* species than have at present been described. Difficulties arise, however, because the plant shows such a wide range of structure and growth pattern even when growing on the same host. Thus normal and giant crusts, with and without trichocytes, with solid and/or creeping crusts, may all grow on one small area of host which would seem to preclude the possibility that they are environmental forms but, at the same time, they are not separable into clearly defined species. In addition, many forms of small *Pneophyllum* spp., such as *P. confervicolum,* may grow in such close association with *Fosliella*, particularly in the tropics, that it becomes impossible to distinguish the separate thalli and identify the entities. It seems that a world wide survey of *Fosliella* based on extensive shore collections coupled with laboratory culture will be essential before the complexity of this genus can be understood. Polyploidy is a possible mechanism which may contribute to the observed variation in giving rise to the giant form. It is also possible that some forms of *Fosliella* may be neotenic forms of more complex mastophoroid genera such as *Neogoniolithon* and *Porolithon.* A more puzzling situation is, as mentioned, the strong resemblance of the germination stages of *Amphiroa* to creeping forms of *Fosliella* even though mature *Amphiroa* has secondary pit connections and belongs to the Amphiroideae.

ECOLOGY: *Fosliella* occurs principally as an epiphyte on other algae and on sea-grasses and may form a dense, floury covering over the host plant. It also grows on pebbles and shells, it is probably less common on these substrata than on plants but few data are available.

DISTRIBUTION: *Fosliella* occurs in tropical and temperate parts of the world (Chamberlain, 1977*b*). It is, however, particularly abundant in warmer climates and absent from colder areas; the British Isles, for example, seems to represent the northern limit of its European distribution.

1a. **Fosliella farinosa** (Lamouroux) M. Howe forma **farinosa**

BASIONYM: *Melobesia farinosa* Lamouroux, *Histoire des polypiers coralligènes flexibles, vulgairement nommés zoophytes*: 315 (1816).

NOMENCLATURAL SYNONYM: *Fosliella farinosa* (Lamouroux) M. Howe, *In* N. L. Britton and C. F. Millspaugh (Eds) *The Bahama flora*: 587 (1920).

REFERENCES: *Melobesia farinosa* Lamouroux; (?) Harvey, *A manual of British algae* 2nd ed.: 109 (1849); Areschoug, *In* J. G. Agardh (Ed.) *Species genera et ordines algarum*: 512 (1852), in *Nova Acta Reg. Soc. scient. Upsala* III, **10**: 366 (1875); Rosanoff in *Mem. Soc. imp. Sci. nat. Cherbourg* **12**: 69 (1866); Foslie in *K. nor. Vidensk. Selsk. Skr.* **1898** (3): 10 (1898), *K. nor. Vidensk. Selsk. Skr.* **1900** (5): 20 (1900), *K. nor. Vidensk. Selsk. Skr.* **1905** (3): 69 (1905) – as f. *typica* and f. *borealis*; Heydrich in *Ber. dt. bot. Ges.* **15**: 44 (1897); Lemoine in *Archs Mus. natn. Hist. nat. Paris* V, **5**: 140 (1913), *In* C. Skottsberg (Ed.), *The Natural History of Juan Fernandez and Easter Island* **2**: 19 (1923*b*); Rosenvinge in *K. dansk. Vidensk. Selsk. Skr.* VII, **7**: 240 (1917); Mazza, *Saggio di Algologia Oceanica* **3**: 1113 (1922); Newton, *A handbook of the British seaweeds*: 300 (1931); Balakrishnan in *J. Indian bot. Soc.* **1946**: 305 (1947 ['1946']); Hamel & Lemoine in *Archs Mus. natn. Hist. nat. Paris* VII, **1**: 102 (1953 ['1952']); Funk in *Pubbl. Staz. zool. Napoli* **25** (Suppl.): 97 (1955); Masaki & Tokida in *Bull. Fac. Fish. Hokkaido Univ.* **11**: 39 (1960); Edelstein & Komarovsky in *Bull. res. Coun. Israel* D, **1–4**: 56 (1961); Lewalle in *Pubbl. Staz. zool. Napoli* **32**: 265 (1961); Zinova, *Check-list of green, brown and red algae of the southern seas of the U.S.S.R.*: 229 (1967); van der Ben in *Proc. int. Seaweed Symp.* **6**: 79 (1969); Pankow, *Algenflora der Ostsee,* I. Benthos: 249 (1971); South in *J. mar. biol. Ass. U.K.* **56**: 820 (1976).

Melobesia farinosa var. *borealis* Lemoine [sic]; Newton, *A handbook of British Seaweeds*: 301 (1931).

Melobesia granulata Meneghini, *In* Zanardini, *Saggio di classificazione naturale delle Ficee*: 44 (1843), Kützing, *Species Algarum*: 696 (1849), *Tabulae Phycologicae*: 34, Tab. 95a, b (1869); Areschoug, *In* J. Agardh, *Nova Acta reg. Soc. scient. Upsala* III, **10**: 518 (1852).

Melobesia zonalis sensu Lemoine in *Archs Mus. natn. Hist. nat. Paris* V, **5**: 140 (1913).

Melobesia minuta Schiffner in *Oesterr. Bot. Zeit.* **82**: 291 (1933).

Fosliella farinosa (Lamouroux) Howe; Feldmann in *Rev. algol.* **11**: 316 (1942 ['1939']); Taylor, *Marine algae of the northern eastern coast of North America* – revised edition: 252 (1957), *Marine algae of the eastern tropical and subtropical coasts of North America*: 388 (1960); Masaki in *Mem. Fac. Fish. Hokkaido Univ.* **16**: 21 (1968); Ganesan, *In*: *Symposium on investigations and resources of the Caribbean Sea and adjacent regions, UNESCO*: 411 (1971); Bressan in *Boll. soc. Adriat. Sci. nat.* **59**: 74 (1974); Parke and Dixon in *J. mar. biol. Ass. U.K.* **56**: 534 (1976); Gordon, Masaki and Akioka in *Micronesica* **12**: 255 (1976); Chamberlain in *Br. phycol. J.* **12**: 343 (1977) – but excluding Figs 5, 6 and 7.

SPECIMENS: *Melobesia farinosa* sensu Le Jolis, no. 282, Cherbourg, coll. 30 Nov. 1853 on *Rhodymenia palmata* (CHE!).

Melobesia membranacea sensu P. Crouan & H. Crouan, exsiccata no. 244 on *Zostera* (CO!).

Lithothamnion membranaceum sensu E. M. Holmes, Sea Mill, Ayrshire, August 1890 on *Zostera* (BM!).

EXCLUDED RECORDS: *Melobesia farinosa* auct. div.; Le Jolis, *Liste des algues marines de Cherbourg*: 150 (1863); Kützing, *Tabulae Phycologicae*: 34, Tab. 95c, d (1869) (both = *Pneophyllum rosanoffii*).

Fosliella farinosa sensu Y. Chamberlain in *Br. phycol. J.* 12: 343 (1977) – Figs 5, 6 and 7 only (= *Pneophyllum concollum*).

HOLOTYPE: CN!, Herb. Lamouroux, from the Mediterranean, growing on *Sargassum linifolium* (Fig. 19).

DIAGNOSIS: Species mainly epiphytic, of thin, bright mauvy-pink crusts, often bleached, terminal hypothallial trichocytes frequent, conceptacles abruptly hemispherical: differing from *Pneophyllum* species by having terminal hypothallial trichocytes and a ring of trichocytes round the base of conceptacles.

DESCRIPTION: Mainly epiphytic bright mauvy-pink crusts (often bleached in summer), probably not individually exceeding 5 mm diameter but confluent and covering large areas of host, often much superimposed, individual crusts up to 20 μm deep, perithallium absent except in immediate vicinity of conceptacles; *crust cells* in surface view elongate, 14–28·5 μm long × 5–16·5 μm wide, *epithallial cells* rounded, 7–13·5 μm long × 3–10 μm wide, hypothallial *trichocytes* terminal, bulbous, 30–43 μm long* × 12–20 μm wide; conceptacles abruptly hemispherical, all (except spermatangial) with simple or slightly elaborated ostiole, *carposporangial conceptacles* 62–100 μm internal diameter × 52–83 μm high, ring of trichocytes round the base, ostiole sometimes with small collar, *spermatangial conceptacles* 33–91 μm internal diameter × 26–44 μm high, ostiole prolonged into a spout, *tetrasporangial conceptacles* as carposporangial conceptacles, 65–94 μm internal diameter × 52–78 μm high, up to 8 tetrasporangia per conceptacle, 36–65 μm long × 23–39 μm wide, some central sterile cells present, young tetrasporangia deeply invaginate, *bisporangial conceptacles* hemispherical, considerably larger than other types, 166–208 μm internal diameter × 45–125 μm high, rarely with ring of trichocytes, 20 or more bisporangia per conceptacle, 54–78 μ long × 26–42 μ wide, central sterile paraphyses present.

HISTORICAL: The taxon now called *Fosliella farinosa* was first described by Lamouroux (1816) as *Melobesia farinosa,* a species of the genus which he had described (Lamouroux, 1812) as a polypore and which was based on Esper's (1806) *Corallina membranacea*. The reasons for the erection of a new genus, *Fosliella*, to accommodate this species are discussed on page 312.

Lamouroux's holotype (CN) of *Melobesia farinosa* (Fig. 19) is an epiphyte on *Sargassum linifolium* from the Mediterranean which is so thickly covered with crusts as to appear floury, hence, presumably, the epithet *farinosa*. I have examined the material and found that many of the crusts agree well with the present concept of *Fosliella farinosa*, these are growing together with crusts of *Pneophyllum* and *Dermatolithon*.

Areschoug (1852) further expanded the description of *Fosliella farinosa* (as *Melobesia*) and pointed out that it was the same taxon as Meneghini's (1843) *Melobesia granulata*. The first detailed anatomical investigation of *Fosliella farinosa*, however, was made by Rosanoff (1866) who observed and illustrated the terminal trichocytes (which he termed heterocysts) for the first time.

Throughout the works of Foslie (1898*b*–1905*a*) *F. farinosa* retained its position in the genus *Melobesia* since he accepted Heydrich's (1897*b*) generic name *Epilithon* for *membranaceum*, and it was generally maintained in *Melobesia* thereafter until Howe's (1920) publication, after which the generic name *Fosliella* was accepted by many authors, although Balakrishnan (1947), Hamel & Lemoine (1953), Kylin (1956), and Masaki & Tokida (1960) are notable exceptions.

Examination of BM material of *Melobesia minuta* Schiffner, growing on *Corallina virgata*, showed it to be *Fosliella farinosa*. As this collection (no. 835) was cited by Schiffner (1933) in the description, it would seem that *Melobesia minuta* must be subsumed in *Fosliella farinosa*.

CRUST APPEARANCE: The bright, mauvy-pink crusts are thin and often become very irregular as parts of them fall off the host. The plants are usually epiphytic on algae (Fig. 38) and *Zostera* but also occur quite frequently on pebbles, glass and shells. The crusts usually show concentric markings and are often confluent covering large areas of the substratum; they may also superimpose (Fig. 22F) to form multi-layered colonies. Individual crusts probably do not exceed 5 mm diameter but are often impossible to measure.

In fresh material the hemispherical conceptacles have a delicate and bubble-like appearance, the bisporangial being noticeably larger than the tetra- and carposporangial conceptacles. Under the S.E.M. mature carposporangial (Fig. 20A) conceptacles have a smooth or regularly stepped pattern of roof cells (sometimes with a small spout round the ostiole) and a ring of trichocytes round the base. Spermatangial conceptacles (Fig. 20E) show a spout surrounded by elongated cells. Observations on developing carpogonial conceptacles under the light microscope (Figs 23A, B) show that the original thallus surface peels off in strips. The bisporangial

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* including the length of the basal cell.

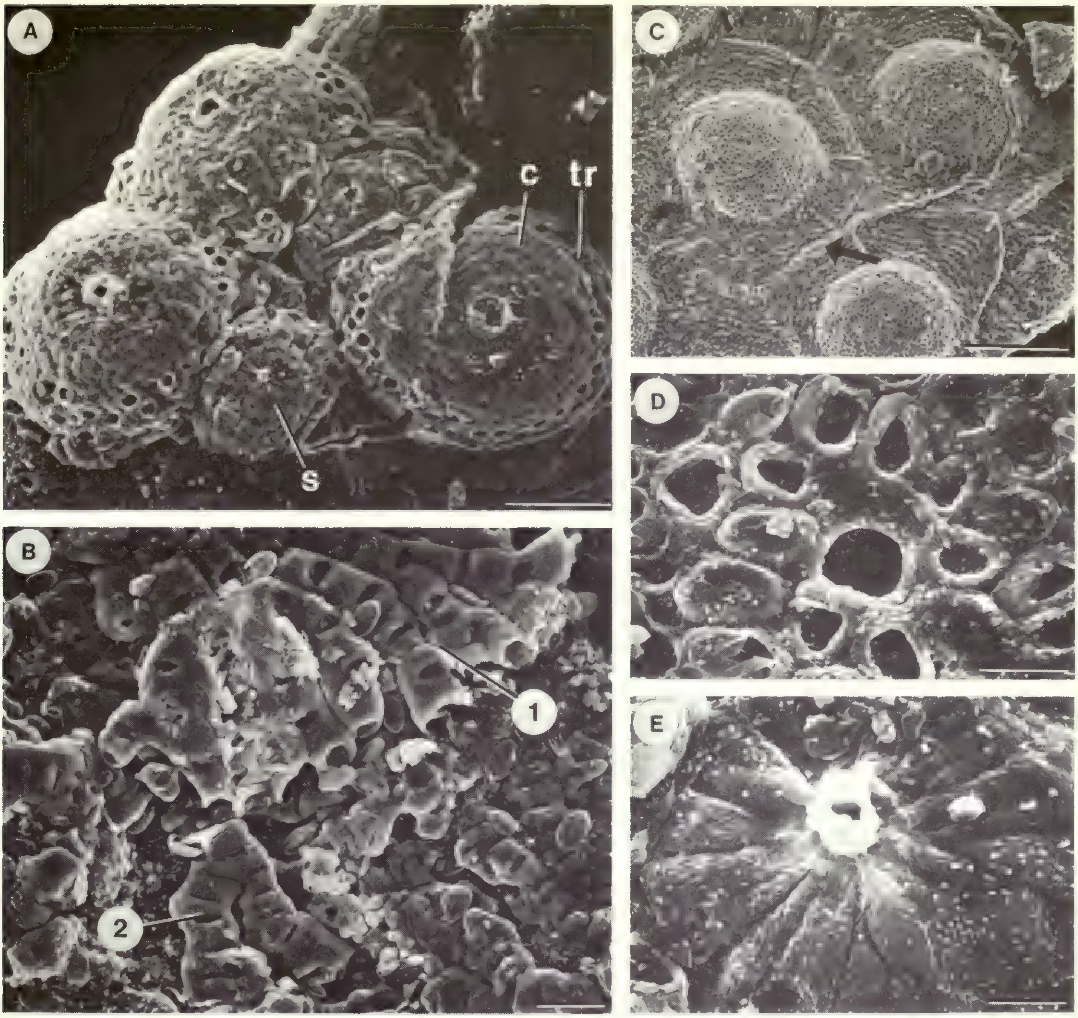


Fig. 20 Scanning electron micrographs to show external features of *Fosliella farinosa*. A, Gametangial crust showing spermatangial conceptacles (s) and carposporangial conceptacles (c) encircled by trichocytes (tr). Scale = 50 μm. B, Creeping filaments of *Fosliella farinosa* f. *callithamnioides* (1) and *Pneophyllum confervicolum* f. *minutulum* (2). Scale = 25 μm. C, Bisporangial crust showing domed conceptacles and ridged thallus (arrow). Scale = 250 μm. D, Ostiole of bisporangial conceptacle. Scale = 10 μm. E, Roof and spout of spermatangial conceptacle. Scale = 10 μm.

conceptacle (Fig. 20C) shows a honeycomb-like surface under the S.E.M., with a rosette of cells (Fig. 20D) surrounding the ostiole (c.f. Garbary, 1978) and each conceptacle is borne on an individual segment of crust which forms a ridge in contact with confluent segments. The crust cells within these segments are relatively shorter than the characteristically elongated peripheral crust cells.

VEGETATIVE ANATOMY: The crusts are composed of hypothallial and epithallial cells, the hypothallial cells are usually radially elongated in surface view while the large, rounded epithallial cells (Fig. 21A) frequently show a conspicuous central nucleus surrounded by radiating crooked canals. In VS the crust cells vary from square to considerably wider than high depending on the angle of the section while the epithallial cells vary from flat to dome-shaped or triangular. The terminal hypothallial trichocytes are bulbous (Figs 10A; 21B), and are usually divided by a wall which appears tangential and anticlinal in surface view but which is somewhat oblique in VS. The centrifugal part of the trichocyte usually bears a long hair (which may branch once, dichotomously) with a thin cell lumen.

Gametangial plants: Gametangial plants are usually monoecious although dioecious plants are found particularly during the winter. When a spermatangial or carpogonial conceptacle is starting to grow a small patch of thickened cells, some of which bear hairs, appears on the thallus surface. As this disc expands, both in width and depth, the original thallus surface peels off in strips (Fig 23A) until the surface of the mature conceptacle is composed entirely of newly developed cells (Fig. 23B) with a ring of trichocytes round the base. In monoecious plants the spermatangial conceptacles are adjacent to the carpogonial conceptacles (Figs 23A, B), their roof is composed of a layer of cells each of which bears an epithallial cell (Figs 22C; 23C), and the cells immediately surrounding the ostiolar spout (Fig. 20E) are radially elongated. Spermatangial initials are borne on the single layer of hypothallial cells which forms the conceptacle base (Fig. 23C) and each gives rise to spermatia from two points. There appear to be two types of spermatangial conceptacle: the larger type (Fig. 22C) measures *c.* 60–90 μm diameter and has elongated spermatia measuring 7–13·5 μm long, while the smaller type (Fig. 23C) measures *c.* 30–50 μm diameter with rounded spermatia *c.* 2–3 μm diameter. Insufficient evidence is available to know whether these types are distinct or extremes of a variation range, but the larger form often occurs on dioecious plants.

Carpogonial conceptacles (Figs 22A; 23A, B, D) are raised and when seen from above (Fig. 23B) the roof cells have a stepped appearance; trichogynes can be seen protruding from the ostiole. The procarps are borne in a bunch in the centre of the conceptacle floor (Figs 22A; 23D) and do not each bear more than a single carpogonium.

Carposporangial conceptacles: Carposporangial conceptacles are regularly hemispherical (Figs 20A; 22B; 23E) and may have a smooth or stepped surface once the original thallus has been shed; in VS (Figs 22B; 23E) the roof is composed of a single layer of cells, each with an

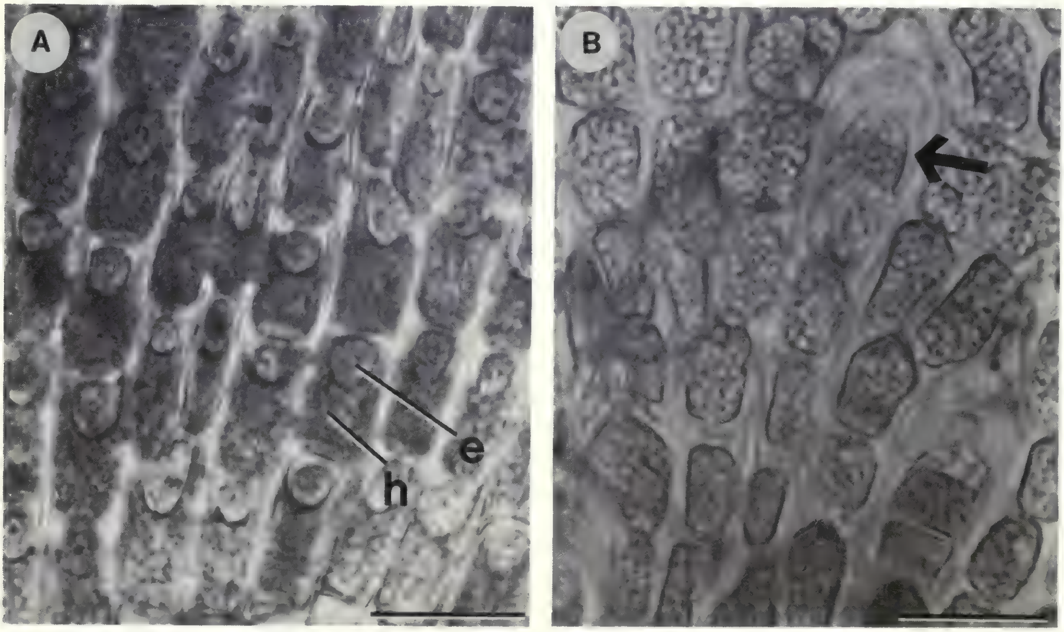


Fig. 21 Surface views of *Fosliella farinosa* crusts. A, Calcified crust showing hypothallial (h) and epithallial (e) cells. Scale = 20 μm. B, Decalcified crust showing terminal trichocyte divided radially into a hair-bearing (arrow) and basal part. Scale = 20 μm.

epithallial cell. The ostiole is sometimes entirely unelaborated but there is usually some development of downwardly-orientated ostiolar filaments (Fig. 23E) and sometimes a small hyaline collar develops round the ostiolar pore. In VS the fusion cell is usually narrow and deep (Figs 22B; 23E), it is often in open contact with the subtending cell (*cf.* Balakrishnan, 1947) and bears substantial remains of carpogonia on its upper surface. Gonimoblast filaments are borne peripherally and are about five cells long.

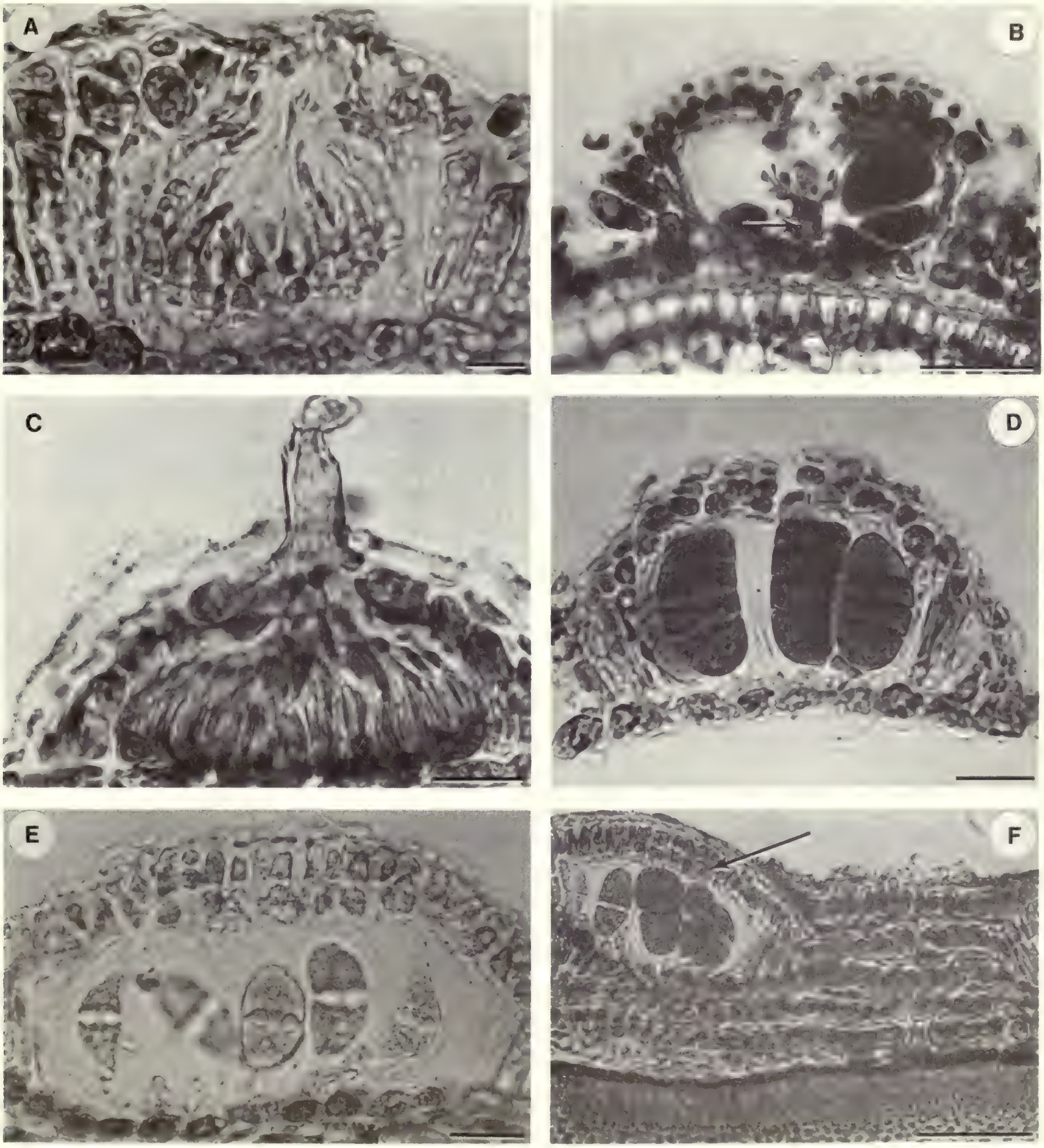


Fig. 22 Vertical sections of *Fosliella farinosa* conceptacles. A, Carpogonial conceptacle. Scale = 20 μm. B, Carposporangial conceptacle showing deep fusion cell (arrow). Scale = 50 μm. C, Large type spermatangial conceptacle. Scale = 20 μm. D, Mature tetrasporangial conceptacle. Scale = 25 μm. E, Immature bisporangial conceptacle. Scale = 25 μm. F, Mature bisporangial conceptacle (arrow) borne on one of five superimposed crusts. Scale = 100 μm.

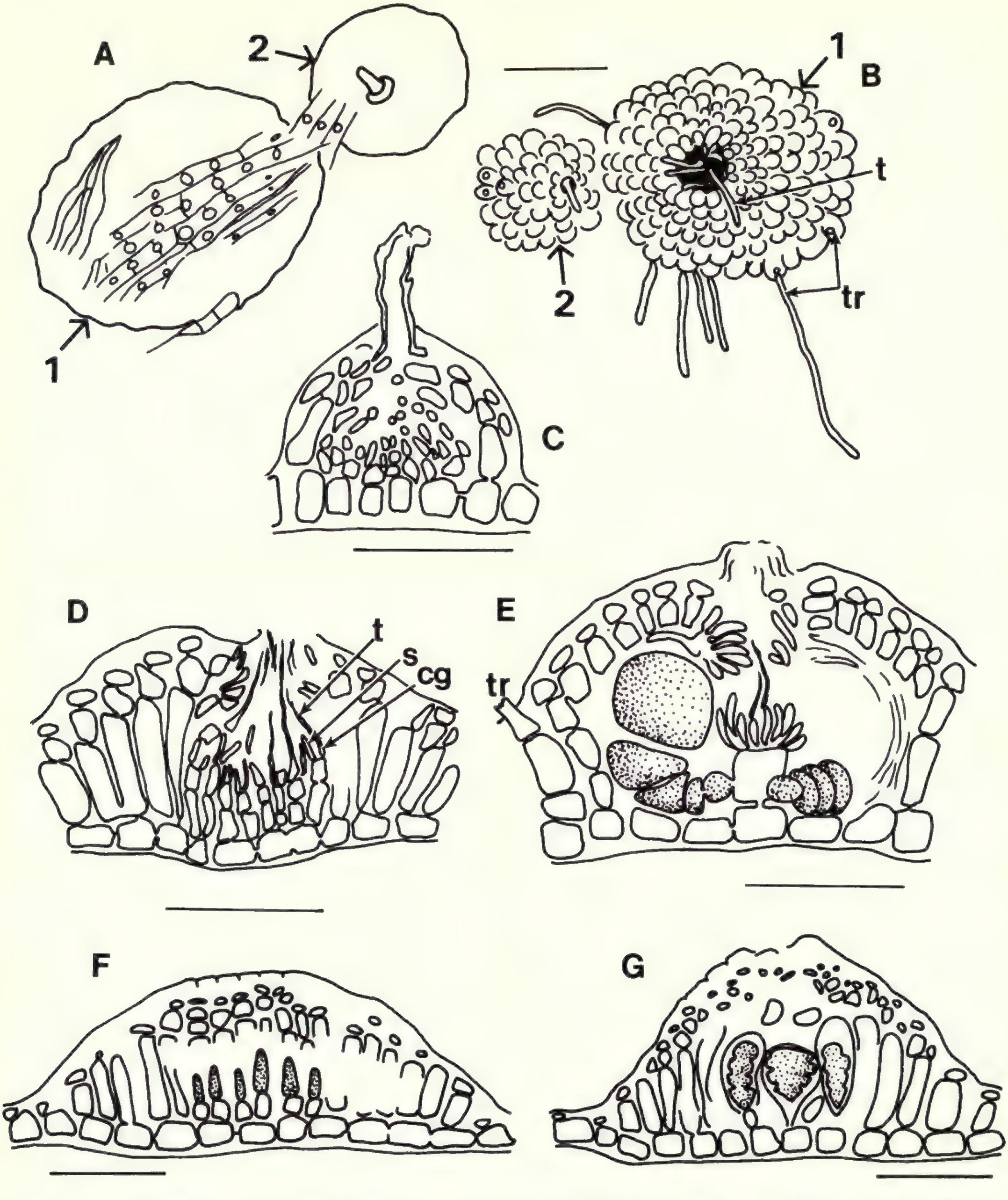


Fig. 23 Gametangial and tetrasporangial conceptacles of *Fosliella farinosa*. A and B, Surface views of developing gametangial conceptacles grown in culture – as seen under the light microscope. A, Young carpogonial (1) and spermatangial (2) conceptacle showing strips of original thallus surface covering parts of the conceptacles. B, Somewhat older conceptacles, after all the thallus has been stripped off, showing the stepped appearance of conceptacle roof cells, the triochocytes round the conceptacle base, and trichogynes protruding from carpogonial ostiole. C–G, Vertical sections. C, Small type of spermatangial conceptacle. D, Carpogonial conceptacle. E, Carposporangial conceptacle. F, Young conceptacle showing tetrasporangial initials (shaded). G, Immature conceptacle showing incompletely divided tetrasporangia within hyaline sacs. All scales = 50 μm. t = trichogyne; cg = carpogonium; s = sterile cell; tr = trichocyte.

TETRASPORANGIAL PLANTS: Conceptacle shape and ostiole structure (Fig. 22D) are similar to that seen in the carposporangial conceptacle. The tetrasporangia are borne peripherally on stalk cells; after initiation (Fig. 23F) immature tetrasporangia (Fig. 23G) become deeply invaginated and do not stain deeply, but when mature they are farctate and stain deeply (Fig. 22D). There are up to about 8 tetrasporangia per conceptacle and there is usually some development of sterile cells in the centre of the conceptacle.

BISPORANGIAL PLANTS: Bisporangial conceptacles are considerably larger than tetra- and carposporangial conceptacles. They have a hemispherical roof (Figs 22E, F), composed of a layer of cells each with a large epithallial cell, the concavity of which gives the roof surface a honeycomb-like appearance under the S.E.M. (Fig. 20C), (see also Garbary, 1978, Figs 16 and 18). A ring of trichocytes has only occasionally been observed round the base of the bisporangial conceptacles and no ostiolar filament development takes place, although a characteristic rosette of cells can be seen round the ostiole in surface view (Fig. 20D).

Twenty or more bisporangia are borne peripherally on stalk cells in each conceptacle and the young sporangia have a curious structure like two toadstools joined by their stalks (Fig. 22E, see also Chamberlain, 1977*b*). Mature tetrasporangia are farctate and stain deeply (Fig. 22F).

PHENOLOGY: *Fosliella farinosa* occurs throughout the year on the shores of the British Isles but, while bisporangial plants occur at all seasons gametangial plants are less common and occur mainly in August and September in warmer areas such as Dorset and southern Ireland. When they occur in winter, gametangial plants are usually abnormal and apparently infertile (Chamberlain, 1977*b*, Figs 8, 9) – a phenomenon also observed by Rosanoff (1866, see Fig. 6 [12]). These observations reflect the geographical variations in this species in that in warmer areas such as the Mediterranean only gametangial/tetrasporangial plants occur, while bisporangial plants (with diploid bispores) are known only from northern France and the British Isles.

FORM RANGE: In addition to the reproductive variations with the season, the crust cells of *F. farinosa* show seasonal differences. Typical crust cells are considerably elongated and the epithallial cells are large and rounded; such cells occur during the summer when the crusts are growing rapidly. In winter, however, the crust cells are smaller in all dimensions (Tab. 6), relatively shorter, and more heavily calcified, while the epithallial cells are smaller and more ovate.

Trichocytes are abundant during warm, light conditions but absent in winter and in deeper subtidal habitats.

DISTRIBUTION:
British Isles: Fosliella farinosa occurs throughout the British Isles, most commonly in southern England and Ireland. The most northerly record of tetrasporangia/gametangia is from Sea Mill, Ayrshire, Scotland where it was collected in August 1890, growing on *Zostera,* by E. M. Holmes (BM). In general, northern populations are probably mainly bisporangial.
World: Recorded from most temperate and tropical parts of the world although, as already mentioned, the taxonomy is somewhat confused. The British Isles records represent the most northerly locality in Europe since the species appears to be absent from Denmark, Sweden, and Norway.

HABITAT: In warmer areas of the world *F. farinosa* is an abundant epiphyte on a wide range of algae and marine angiosperms on which it forms a dense powdery covering of closely crowded crusts smothered with conceptacles; in the intertidal zone the crusts are usually bleached. This type of covering is not usually seen in the colder parts of Britain, but has been noted in warmer localities such as Kimmeridge and Lough Ine. *F. farinosa* is also common on many algal hosts as well as on *Zostera* in the warm waters of the Fleet in Dorset.

F. farinosa is, however, present throughout the year in most parts of the British Isles as mauvy-pink, often extensive, confluent crusts on many intertidal algae, but particularly on the tophules of *Cystoseira nodicaulis* and the fronds of *Chondrus crispus*. It also frequently forms a

Table 6 Dimensions of vegetative structures (in μm unless stated).

Fosliella farinosa	British Isles	Hamel & Lemoine (1953)	Masaki & Tokida (1960)	Ganesan (1971)
crust diameter	up to *c.* 5mm		2–4mm	1–5mm
crust depth	*ca.* 20			
crust cell length	(14) 20·5 (28·5) (8·5) 14 (20)*	(9) 10–20 (22)	12–20	
surface width	(5) 10 (16·5) (5) 7·5 (11)	(5) 7–12 (18)	5–9	
crust cell height	9–12	8–14	5–13	
epithallial cell length	(7) 9 (13·5) (2·5) 4 (6)*	rounded		
surface view width	(3) 7 (10) (2) 4 (6)*			
epithallial cell height	*c.* 5–8			
hypothallial cell width			7–13	15–30
VS height			5–13	(6) 9–12 (15)
perithallial width				
cell height				
VS number				
trichocyte type	terminal	terminal	terminal	terminal
trichocyte length	(30) 35 (43)	17–30 (43)	20–25	14–25 (35)
surface view width	(12) 16 (20)	12–18 (30)	7–10	(6) 8–12 (15)

RIDGWAY COLOUR CODE: dry crust – light vinaceous lilac, Pl. XLV

Table 7 Dimensions of reproductive structures (μm unless stated).

Fosliella farinosa f. *farinosa*	British Isles	Hamel & Lemoine (1953)	Masaki & Tokida (1960)	Ganesan (1971)
CARPOSPORANGIAL CONCEPTACLE				
external diameter		140–200 (250)	(29) 105–126	218–300
surface diameter	(91) 99 (104)			
VS internal diameter	(62) 85 (110)		(29) 105–126	110–145
VS height	(52) 63 (83)		(25) 42–63 (91)	58–87
VS roof height	(13) 16 (18)			
roof type	irregular			
no. basal cell rows	1			
ostiole	simple or tiny spout	small corona		
no. gonimoblast filaments	5–10			
diameter carpospore				*c.* 30
SPERMATANGIAL CONCEPTACLE				
VS/surface width	(33) 76 (91)	60–80	(42) 55–84	
VS height	(26) 37 (44)		(29) 33–46 (55)	
length spermatium	(7) 10 (13·5)		3–7	
width spermatium	1·5–3 (or rounded 2–3 μm diam.)		2	

* dimensions in winter-collected material

TETRASPORANGIAL CONCEPTACLE				
external diameter		140–200 (250)	(84) 126–168 (189)	230–300
surface	(78) 114 (130)			
VS internal diameter	(65) 86 (94)			
VS height	(52) 66 (78)		63–126	
VS roof height	(10) 15 (20)			
roof type	irregular			
no. basal cell rows	1			
ostiole	simple or tiny spout	small corona		
no. tetrasporangia	*c.* 8		3–7	4–7
length tetrasporangium	(36) 42 (65)	50–90	40–80	32–58
width tetrasporangium	(23) 30 (39)	30–50	(20) 25–50 (63)	35–44
BISPORANGIAL CONCEPTACLE				
external diameter		140–200 (250)		
surface diameter	(156) 193 (216)			
VS internal diameter	(166) 187 (208)			
VS height	(45) 89 (125)			
VS roof height	(18) 30 (39)			
roof type	zonal			
no. basal cell rows	1			
ostiole	simple rosette			
no. bisporangia	20+			
length bisporangium	(54) 65 (78)	45–55		
width bisporangium	(26) 34 (42)			

bloom, together with *Pneophyllum limitatum*, on a range of intertidal algae such as *Palmaria palmata, Laminaria* spp. and *Fucus serratus* from September until about November, depending on the weather conditions (Chamberlain, 1982). Herbarium specimens such as Le Jolis's (exsiccata no. 282 on *Rhodymenia palmata* 30 November 1853 [CHE]) indicate that a similar bloom occurs in northern France.

LIFE HISTORY: A self-perpetuating bisporangial life history was established for *Fosliella farinosa* in laboratory culture (Chamberlain, 1977*b*). In addition, tetraspores were germinated and grown in von Stosch culture medium to produce monoecious crusts bearing spermatangial and carpogonial conceptacles (Figs 23A, B), but the carpogonia apparently remained unfertilised and the carposporangial phase did not develop.

1b. **Fosliella farinosa** forma **callithamnioides** (Foslie) Y. Chamberlain, **comb. nov.**

BASIONYM: *Melobesia farinosa* f. *callithamnioides* Foslie in *K. nor. Vidensk. Selsk. Skr.* **1905** (3): 96 (1905), non *M. callithamnioides* (P. Crouan & H. Crouan) Falkenb.

NOMENCLATURAL SYNONYMS: *Melobesia solmsiana* Falkenb. in *Fauna Flora Golf Neapel* **26**: 109 (1901). *Melobesia farinosa* f. *solmsiana* (Falkenb.) Foslie in *K. nor. Vidensk. Selsk. Skr.* **1908** (7): 16 (1908).

REFERENCES: *Melobesia callithamnioides* Falkenb. in *Mitt. zool. Stn Neapel* **11**: 265 (1879); Hauck, *Die Meeresalgen*: 262 (1885); Solms-Laubach in *Fauna Flora Golf Neapel* **4**: 11 (1881); Heydrich in *Ber. dt. Boi Ges.* **15**: 44 (1897).
Melobesia farinosa f. *callithamnioides* (Falkenb.) Foslie; Zinova, *Check-list of green, brown and red algae of the southern seas of U.S.S.R.*: 229 (1967).
Melobesia farinosa var. *callithamnioides* Foslie; Newton, *A handbook of the British seaweeds*: 301 (1931).
Melobesia farinosa f. *solmsiana* (Falkenb.) Foslie; Lemoine in *Dansk. bot. Arkiv.* **3**: 171 (1917); Hamel & Lemoine in *Archs Mus. natn. Hist. nat. Paris* VII, **1**: 102 (1953['1952']); Cabioch, *In* Feldmann in *Trav. Stn biol. Roscoff* II, **15**: 17 (1964).
Fosliella farinosa var. *solmsiana* (Falkenb.) Feldmann in *Rev. algol.* **11**: 316 (1942 ['1939']); Taylor, *Marine*

algae of the eastern tropical and subtropical coasts of North America: 389 (1960); Cabioch in *Bull. Soc. phycol. Fr.* **19**: 78 (1974); Bressan in *Boll. Soc. adriat. Sci. nat.* **59**: 79 (1974).

EXCLUDED RECORDS: *Hapalidium callithamnioides* P. Crouan & H. Crouan in *Annals Sci. nat. Bot.* IV, **12**: 287 (1859).

Guerinia callithamnioides (P. Crouan & H. Crouan) Picquenard in *Trav. scient. Lab. Zool. Physiol. marit. Concarneau* **4** (3): 1 (1912) (= *Pneophyllum confervicolum* f. *minutulum q.v.*).

TYPE SPECIMEN: See text.

DIAGNOSIS: Differing from f. *farinosa* in having filamentous thalli.

DESCRIPTION: Forming creeping, filamentous thalli, with gametangial and tetrasporangial conceptacles only.

HISTORICAL: *Fosliella farinosa* f. *callithamnioides* was first recorded from the Gulf of Naples by Falkenberg (1879) as *Melobesia callithamnioides* (Crouan frat.) since he thought it was the taxon described by the Crouans (1859) as *Hapalidium callithamnioides*. Solms-Laubach (1881) subsequently recorded and figured the taxon under the name *Melobesia callithamnioides*. Later, Falkenberg (1901) concluded that his own and Solms-Laubach's material was a different taxon from that described by the Crouans and he therefore erected a new species, *Melobesia solmsiana*, to accommodate the entity.

Foslie (1905*a*), however, considered Falkenberg's species to be a form of *Melobesia farinosa* and recorded it as '*M. farinosa* f. *callithamnioides* (Falkenb.) Foslie'. The attribution to Falkenberg is, however, incorrect, because he was simply using the Crouans' taxon, as explained above. Since Foslie's (1905*a*) publication was the first use of the name for the rank of form (and which excluded *Hapalidium callithamnioides* as a synonym) the basionym should be cited as *Melobesia farinosa* f. *callithamnioides* Foslie (1905*a*). Foslie refers to Falkenberg's and Solms-Laubach's publications but apparently did not see their material, and I have not been able to locate either of their specimens. The lectotype could therefore either be chosen from among the specimens which Foslie had seen (Wille-Mediterranean, Sauvageau–Tenerife; Howe-Caribbean) or Solms-Laubach's illustration could be used for this purpose. Since Falkenberg (1901) clearly agreed with Solms-Laubach's identification and publication, the last solution seems preferable.

GENERAL COMMENTS: As previously remarked (p. 333) it is possible that the creeping filaments (Fig. 20B) of f. *callithamnioides* may not be genetically distinct from f. *farinosa*, nevertheless this growth form has been widely reported, particularly from warm water areas such as the Mediterranean. Since its appearance is so distinctive it is considered valuable to retain its identity as a named forma.

DISTRIBUTION:
British Isles: Co. Cork.
World: Mediterranean; Caribbean; southern U.S.S.R.

HABITAT: Plants of f. *callithamnioides* (Fig. 20B) have been noted on only one occasion – at Lough Ine growing on turf-like communities of *Gelidium pusillum* and other algae. The creeping forms of *Fosliella farinosa* occur principally in warmer waters and Lough Ine shore conditions bear some resemblance to those found in the Mediterranean, as indicated by the fact that southern Ireland is the only British Isles habitat for the sea urchin *Paracentrotus lividus* (Lamarck). This sea urchin is common in the Mediterranean (Goss-Custard *et al.*, 1979).

II. *Pneophyllum*

Pneophyllum Kütz., *Phycologia generalis*: 385 (1843).

TYPE SPECIES: *Pneophyllum fragile* Kütz., *Phycologia generalis*: 385 (1843).

HOLOTYPE: L! no. 941.241.152, Herb. Kützing, from the Mediterranean, growing on *Sphaerococcus coronopifolius* (Fig. 24).

Synonymy: There are no nomenclatural synonyms of *Pneophyllum,* but *Hapalidium* sensu P. Crouan & H. Crouan (1859) non Kütz., and *Heteroderma* Foslie (1909) are taxonomic synonyms.

Description: *Thallus* calcified, crustose, either epiphytic on algae and marine angiosperms, or epilithic on stones, glass and rocks, or epizoic on shells; vegetative thallus either composed of hypothallium and epithallium only or with perithallial filaments up to 12 or more cells deep, cell fusions frequent, hypothallial *trichocytes* (when present) normally intercalary, occasional abnormal very large terminal trichocytes present. *Gametangial plants* monoecious, carpogonial

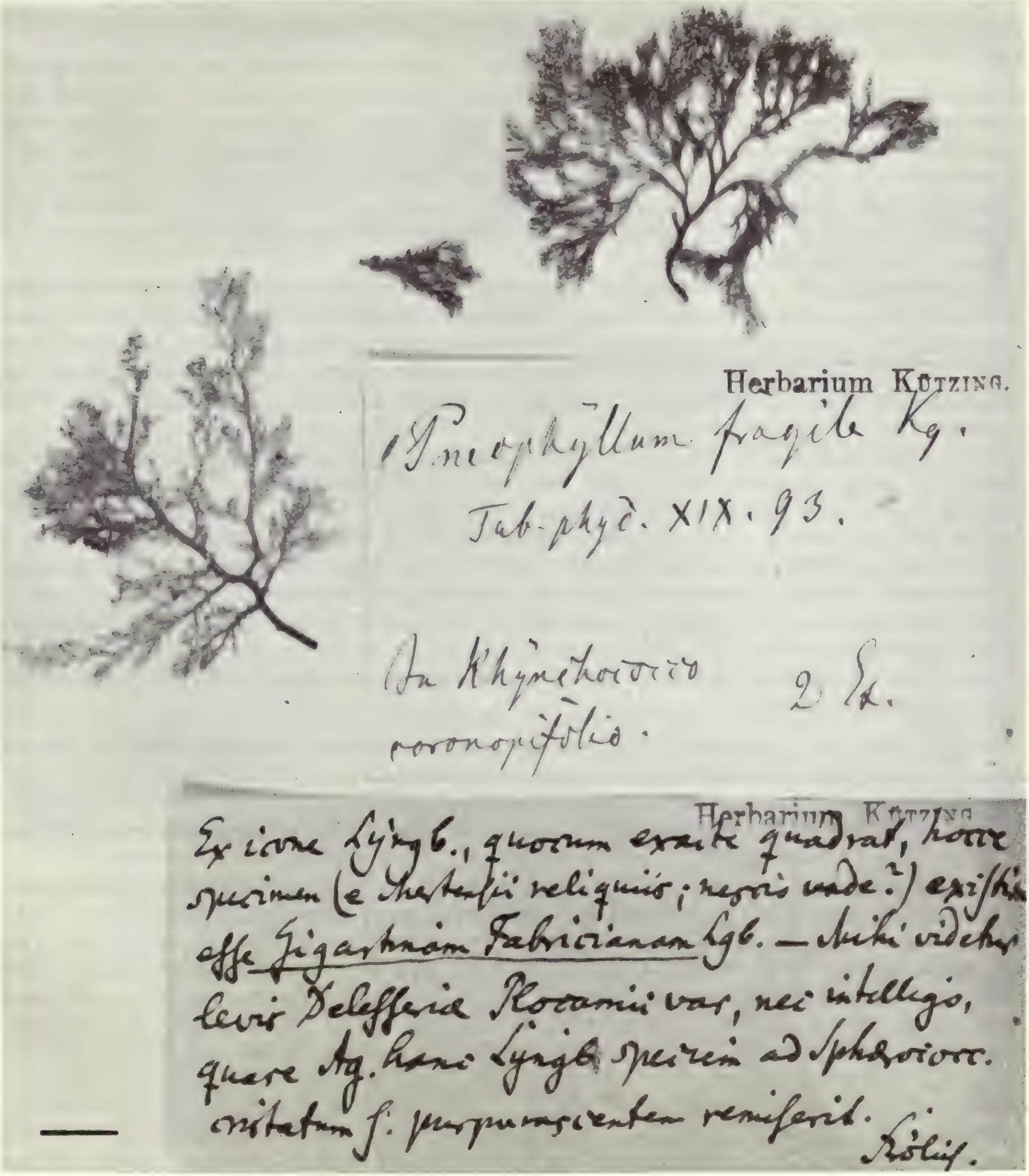

Herbarium Kützing.
Pneophyllum fragile Kg.
Tab. phyc. XIX. 93.
An Rhynchococco coronopifolio. 2 Ex.
Herbarium Kützing
Ex icone Lyngb., quorum exacte quadrat, hocce specimen (e Shetlandii reliquiis; negotio vade?) existit esse Gigartinam Fabricianam Lgb. — Mihi videtur levis Delesseria Hookerii var, nec intelligo, quare Ag. hanc Lyngb. speciem ad Sphaerococc. cristatum f. purpurascentem remiserit.

Fig. 24 Type specimen of *Pneophyllum fragile* (L no. 941.241.152); the frond bearing the *Pneophyllum* crusts is on the left. Scale = 10 mm.

conceptacles raised to immersed, with central ostiole through which trichogynes protrude, fertile procarps bearing one or two carpogonia; spermatangial conceptacles immersed, ostiole prolonged into a spout. *Carposporangial conceptacles* prominent or immersed, ostiole simple, or with corona of free filaments, or with filaments fused into a collar, funnel or dome, roof uniform, irregular or zonal; fusion cell not in open connection with subtending thallus cells. *Tetrasporangial plants* with single-pored conceptacles similar to carposporangial conceptacles, tetrasporangia borne peripherally on stalk cells, usually some development of central sterile cells. *Bisporangial plants* with uninucleate (presumably diploid) bispores, conceptacles similar to tetrasporangial ones. *Spore germination disc* with central element of eight cells, the four central cells initiating one hypothallial filament each, the four peripheral cells initiating two hypothallial filaments each.

HISTORICAL: The genus *Pneophyllum*, in the family Spongitae (i.e. crustose corallines), was proposed by Kützing (1843) to accommodate the single species *P. fragile*, which had a thallus of two cell layers; the upper, cortical cells (i.e. epithallium) were much smaller than the lower layer of somewhat rounded cells (i.e. hypothallium). This distinguished it from: a) *Hapalidium* which Kützing thought had only a single cell layer; b) *Melobesia* (i.e. *Dermatolithon*) which had very elongated lower cells; and c) *Spongites* (i.e. complex crusts including *Lithothamnium* and *Lithophyllum*) with many cell layers.

For some reason the name *Pneophyllum* has never been taken up, possibly because the status of the single species has remained obscure. However, Kützing's specimen (Fig. 24) is in good condition, and can be assigned without doubt to the taxon under discussion. On grounds of priority, therefore, the name *Pneophyllum* is applied to the present genus. Further discussion on the interpretation of Kützing's work on simple crustose coralline algae is given on p. 298, while his specimen of *P. fragile* is described here in detail for the first time.

Species belonging to *Pneophyllum*, as now defined, have been mainly assigned to *Melobesia* since 1843; other genera to which they have been attributed include *Hapalidium, Dermatolithon, Lithocystis, Heteroderma, Guerinea,* and *Fosliella* (Tab. 1). The nomenclature of species now assigned to *Pneophyllum* suffered numerous changes in the course of Foslie's publications and these are demonstrated in Table 3. Foslie's (1909) final circumscription of *Heteroderma*, however, as simple crustose species lacking trichocytes is essentially the same as that of *Pneophyllum*. Foslie recognised the terminally situated hyaline cells of *Fosliella farinosa* (which he assigned to the monotypic genus *Melobesia*) as trichocytes; he did not consider the hyaline intercalary cells (which he observed in some species of *Heteroderma*) to be essentially the same type of structure.

SYSTEMATICS: About 20 species of *Pneophyllum* have been described mostly under the generic names *Fosliella* and *Heteroderma*. The species vary from those with only a hypothallium and epithallium in the vegetative parts of the thallus (e.g. *P. lejolisii* and *P. confervicolum*) to thalli up to 12 or more cells deep (e.g. *Fosliella chamaedoris* (Foslie & M. Howe) E. Dawson (1960, p. 54) and *P. plurivalidum* (*q.v.*).

The relationship of *Pneophyllum* to the more complex crustose mastophoroideaen genera, such as *Neogoniolithon* and *Porolithon*, which have many hypothallial layers and a deep perithallium, is not yet clear. There is, however, a group of species which may represent an intermediate stage between *Pneophyllum* and these genera. These species are simpler than *Porolithon* and *Neogoniolithon*, have a single or a few hypothallial layers and a more developed perithallium than is seen in *Pneophyllum*. The species are at present grouped in *Pseudolithophyllum* sensu Adey (see Fig. 16). Adey (1970) lists 22 species in the taxon, but information about many of these is sparse, and there is a lack of knowledge as to whether the tetrasporangial conceptacles are single- or many-pored. Until more information is available and the nomenclatural tangle between *Pseudolithophyllum* sensu Lemoine, a lithophylloid genus, and the mastophoroid *Pseudolithophyllum* sensu Adey is resolved, it is not beneficial to theorise further on the possible relationships amongst these genera.

ECOLOGY: *Pneophyllum* probably occurs mainly as an epiphyte on other algae and sea-grasses; it also, however, occurs epilithically and epizoically, and may be common in these forms but very few data are at present available.

Probably the most familiar association which includes *Pneophyllum* species is the sea-grass epiphyte association, which has been studied by workers such as van der Ben (1969) in the Mediterranean and Brauner (1975) in North Carolina. The species most commonly found on sea-grasses is *P. lejolisii* which probably occurs in most parts of the world.

DISTRIBUTION: *Pneophyllum* probably occurs in seas throughout the world outside the polar regions.

Key to species of *Pneophyllum* in the British Isles

1	Epiphytic	2
–	Epilithic or epizoic	11
2(1)	Vegetative crust of hypothallium and epithallium only	3
–	Vegetative crust, at least in older parts, with perithallium	6
3(2)	Conceptacles flattened, ostiole simple, occurring on *Zostera* only	**2. P. lejolisii** (p. 358)
–	Conceptacles prominent	4
4(3)	Conceptacles with long, free, ostiolar filaments	**3. P. rosanoffii** (p. 367)
–	Conceptacles not with long, free, ostiolar filaments	5
5(4)	Conceptacles less than 100 μm internal in diameter, ostiole simple	**5. P. confervicolum** (p. 383)
–	Conceptacles more than 100 μm internal in diameter, ostiole funnel-shaped	**4. P. limitatum** (p. 374)
6(2)	Conceptacles with simple ostiole	7
–	Conceptacles with ostiolar filaments or collar	9
7(6)	Conceptacles with dark centre	**12. P. sargassi** (p. 445)
–	Conceptacles of uniform colour, often densely crowded	8
8(7)	Carpo-, tetra- and bisporangial conceptacles all small, immersed	**6. P. microsporum** (p. 395)
–	Only bisporangial conceptacles small, immersed (other types conical)	**4. P. limitatum** (p. 374)
9(6)	Conceptacles with ostiolar filaments fused into a collar (epiphytic on *Palmaria* or other algae)	**7. P. concollum** (p. 402)
–	Conceptacle with long, free, ostiolar filaments	10
10(9)	Conceptacle roof (in VS) of one large and two small cell layers, ostiolar filaments terete (epiphytic on *Halopitys, Palmaria*, other algae and *Zostera*)	**3. P. rosanoffii** (p. 367)
–	Conceptacle roof (in VS) many small cells thick, ostiolar filaments flattened, wispy (found epiphytically only on *Chondrus*)	**11. P. zonale** (p. 433)
11(1)	Vegetative crust of hypothallium and epithallium only	12
–	Vegetative crust, at least in older parts, with perithallium	13
12(11)	Conceptacles flat, with a simple ostiole	**2. P. lejolisii** (p. 358)
–	Conceptacles conical, with a collar-like ostiole	**8. P. myriocarpum** (p. 410)
13(11)	Conceptacles prominent, with long, free, flattened, wispy, ostiolar filaments	**11. P. zonale** (p. 433)
–	Conceptacles immersed (at least when fresh), not with long, free, ostiolar filaments	14
14(13)	Perithallium up to 6 cells deep, conceptacles in dried crust pale and merging gradually into darker thallus; thallus frequently lobed	**9. P. lobescens** (p. 419)
–	Perithallium up to 8 cells deep, conceptacles in dried crust discrete white circles, often with a pink centre; thallus not becoming lobed	**10. P. plurivalidum** (p. 427)

1. **Pneophyllum fragile** Kütz., *Phycologia generalis*: 385 (1843).

BASIONYM: *Pneophyllum fragile* Kütz., *Phycologia generalis*: 385 (1843).

REFERENCES: *Pneophyllum fragile* Kütz., *Phycologia Germanica*: 295 (1845), *Tabulae phycologicae*: 33, Tab. 93 a–c (1869); Kylin, *Die Gattungen der Rhodophyceen*: 560 (1956).

Melobesia pruinosa (?) Kütz., *Phycologia Germanica*: 295 (1845).

HOLOTYPE: L! no. 941.241.152, Herb Kützing, from the Mediterranean (or Adriatic?), growing on *Sphaerococcus coronopifolius* (Fig. 24).

DIAGNOSIS: Species epiphytic on *Sphaerococcus coronopifolius,* of thin, pale crusts with intercalary trichocytes, conceptacles slightly raised, ostiole simple: differing from *Pneophyllum lejolisii* by being epiphytic on algae as well as seagrasses and having relatively narrow tetrasporangia.

DESCRIPTION: Epiphytic, very pale (probably bleached with age), thin crusts not exceeding 1·5 mm diameter, crusts up to 50 μm deep, perithallium absent except in immediate vicinity of conceptacles; *crust cells* relatively broad in surface view, 6·5–10·5 μm long × 5–10 μm wide, intrafilament *trichocytes* 8–12 μm long × 8·5–9·5 μm wide; conceptacles somewhat raised, all (except spermatangial) with simple ostiole, *carposporangial conceptacles c.* 85 μm internal diameter × 45 μm high, *spermatangial conceptacles c.* 28 μm wide × 20 μm high, ostiole prolonged into a spout, *tetrasporangial conceptacles* as carposporangial conceptacles, 90–100 μm internal diameter, *c.* 45 μm high, tetrasporangia peripheral, probably *c.* 10 per conceptacle, 30–39 μm long × 18–25 μm wide.

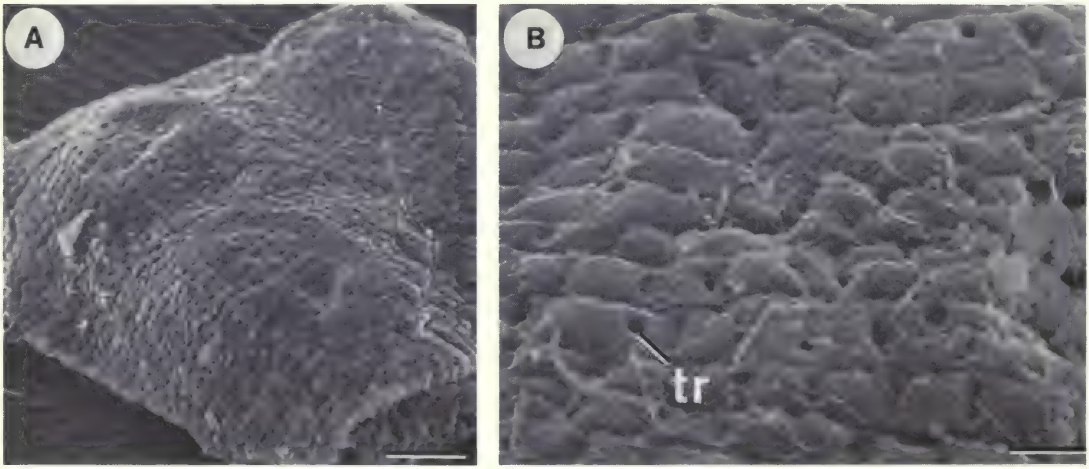


Fig. 25 Scanning electron micrographs of the type specimen of *Pneophyllum fragile*. A, Young conceptacles. Scale = 50 μm. B, Crust cells with trichocytes (tr). Scale = 10 μm.

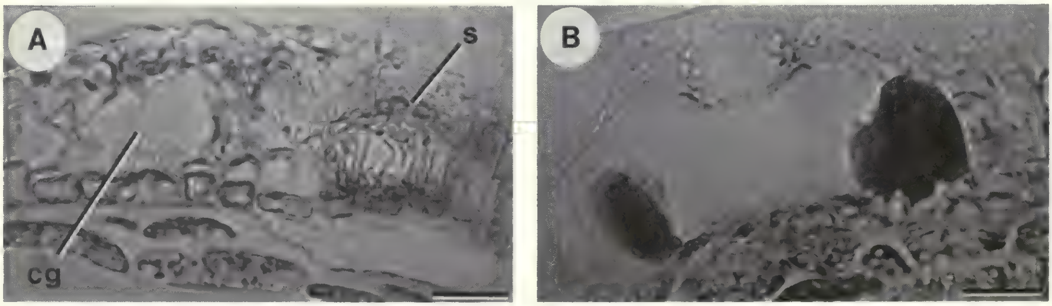


Fig. 26 Vertical sections of *Pneophyllum fragile* conceptacles. A, Gametangial crust showing spermatangial (s) conceptacle and edge of carpogonial conceptacle (cg). Scale = 20 μm. B, Carposporangial conceptacle with obliquely cut ostiole. Scale = 20 μm.

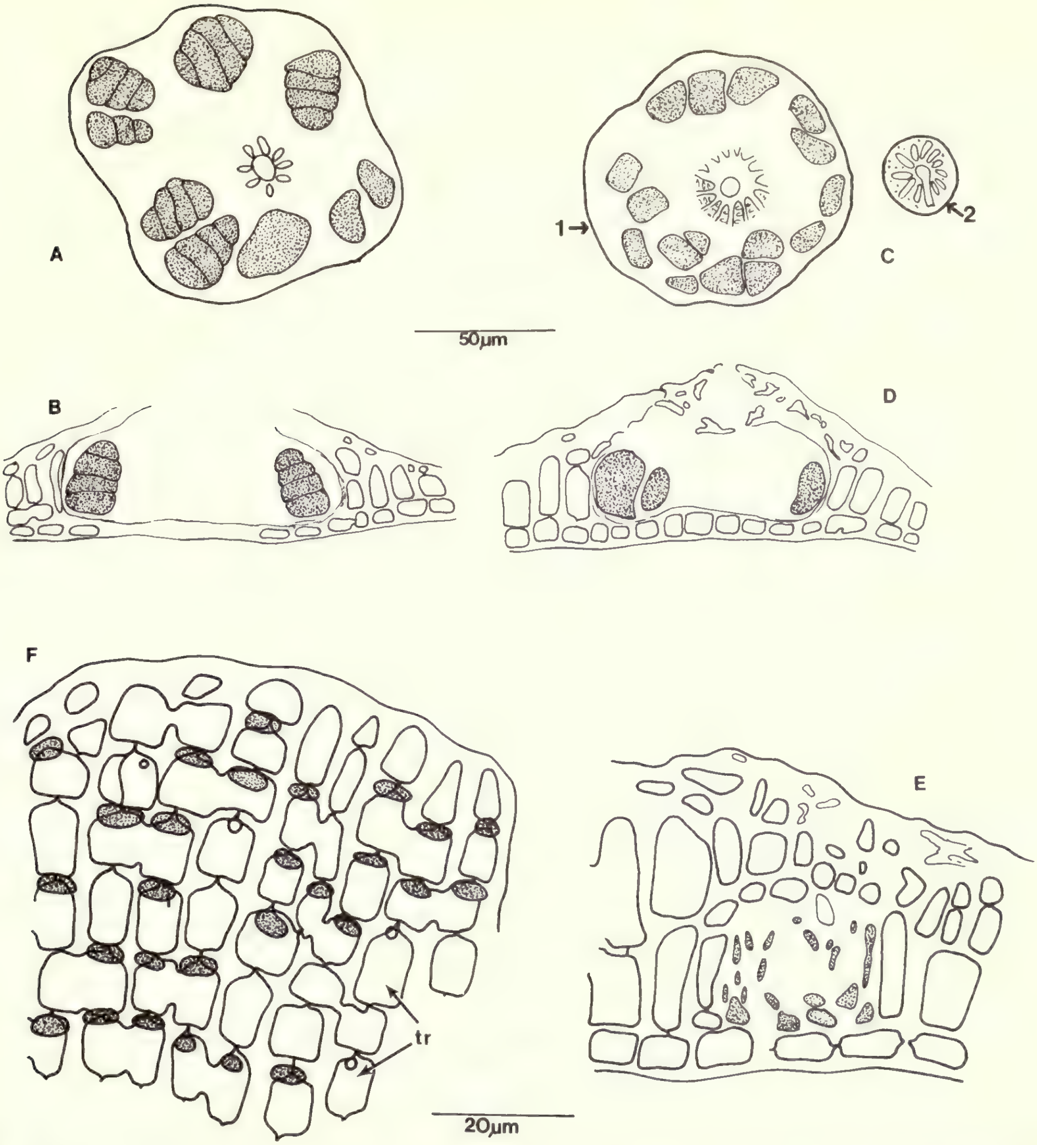


Fig. 27 Decalcified preparations of *Pneophyllum fragile*. A, Surface view of tetrasporangial conceptacle showing the peripheral tetrasporangia and the central position of the ostiole surrounded by a rosette of cells. B, Vertical section of tetrasporangial conceptacle (reconstructed). C, Surface view of carposporangial conceptacle (1) with central ostiole and spermatangial conceptacle (2) with spout. D, Vertical section of carposporangial conceptacle. E, Vertical section of spermatangial conceptacle. F, Surface view of crust with intrafilament trichocytes.

HISTORICAL: Kützing described the genus *Pneophyllum* in 1843 (see p. 300) based on the single species *P. fragile,* the type specimen (Fig. 24) of which is epiphytic on *Sphaerococcus coronopifolius* L no. 941.241.152). The locality (Kützing, 1843) is given as 'Im Mittelmeere' and it was probably collected by Kützing on his visit to the Adriatic and Mediterranean in 1835 (Ducker, 1981). Later, however, Kützing (1845) recorded *P. fragile* as being 'An *Rhyncococcus coronopifolius* und anderen Tange an der Dalmatischen Küste' so he was probably using 'Mediterranean' in the widest sense in 1843. The crusts of *P. fragile* are mixed with crusts of *Fosliella farinosa* and

Table 8 Dimensions of vegetative structures (in μm unless stated).

Pneophyllum fragile	Type specimen
crust diameter	*c.* 1·5 mm
crust depth	*c.* 40–50
crust cell length	(6·5) 9 (10·5)
surface width	(5) 7 (10)
crust cell height	*c.* 15
epithallial cell length	(1·5) 2·5 (3·5)
surface view width	(3·5) 5 (7·5)
epithallial cell height	
hypothallial cell width	
VS height	
perithallial width	
cell height	
VS number	
trichocyte type	intrafilament
trichocyte length	8–12
surface view width	8·5–9·5

Table 9 Dimensions of reproductive structures (μm unless stated).

Pneophyllum fragile	Type specimen
CARPOSPORANGIAL CONCEPTACLE	
external diameter	
surface diameter	85–90
VS internal diameter	85
VS height	45
VS roof height	
roof type	uniform
no. basal cell rows	1
ostiole	simple
no. gonimoblast filaments	
diameter carpospore	
SPERMATANGIAL CONCEPTACLE	
VS/surface width	28
VS height	20
length spermatium	
width spermatium	
TETRASPORANGIAL CONCEPTACLE	
external diameter	
surface diameter	110–112
VS internal diameter	95–100
VS height	45
VS roof height	
roof type	uniform
no. basal cell rows	1
ostiole	simple
no. tetrasporangia	*c.* 10
length tetrasporangium	30–39
width tetrasporangium	18–25

Dermatolithon on *Sphaerococcus*, and the reasons for considering that it was not these two genera to which Kützing was referring in his description of *Pneophyllum fragile* are discussed on p. 300.

There is only one other sample originally labelled *P. fragile* by Kützing in his herbarium and this is a mixture of epiphytic crusts including *P. lejolisii, P. rosanoffii*, and *Dermatolithon* growing on a sea-grass collected in the Adriatic (L no. 941.241.153). Together with this specimen, however, is a small packet originally labelled '*Pneophyllum pruinosam* Kg. Auf *Sphaerat. nervosus* Ragusa' which is a mixture of *Melobesia membranacea* and *Dermatolithon* spp. Kützing subsequently crossed out *pruinosam* and inserted *fragile*. *Melobesia pruinosa* was described by Kützing (1845) as growing on *Zostera* at Trieste and being composed of thin, pale grey, confluent crusts with very small, tightly packed conceptacles. This species was never mentioned again by Kützing and there is no specimen still labelled with this name in his herbarium.

On the basis of Kützing's specimens and publications mentioned above, I have come to the following conclusions: 1) Kützing originally regarded *Pneophyllum fragile* as a very thin crust growing on *Sphaerococcus*, and *Melobesia pruinosa* as a thin crust growing on *Zostera,* and 2) Kützing subsequently decided that these two entities were the same taxon and should be known as *Pneophyllum fragile* which, therefore, grew on both algae and sea-grasses.

Examination of the type material of *P. fragile* shows it to be very similar to the species now known as *P. lejolisii*, but this species is confirmed only as growing on sea-grasses and (very occasionally) epilithically. Various authors record it as being epiphytic on algae (e.g. Woelkerling, 1975, from the Sargasso Sea; Cormaci & Furnari, 1979, from Sicily; Bressan, 1974, from Italy – all as *Fosliella*). I have not, however, been able to see any material to substantiate these records, and as the type material is scanty and mostly immature I cannot be certain that *P. fragile* and *P. lejolisii* are the same taxon; it seems preferable, therefore, to keep them distinct at least until positive evidence that *P. lejolisii* grows on algal hosts in the Mediterranean and Adriatic is available.

General comments: From the sparse material of *P. fragile* available it can be seen to be composed of thin crusts with rather broad crust cells (Figs 25B, 27F), and short broad epithallial cells. Intrafilament trichocytes are common and are larger than surrounding crust cells. The conceptacles (Figs 26; 27B, D, E) are mainly somewhat raised; all those seen under the S.E.M. (Fig. 25A) are immature and no ostiole structure is visible; surface mounts of decalcified conceptacles suggest, however, that a rosette of cells may sometimes surround the ostiole (Figs 27A, C). In VS (Figs 26B, 27D) the ostiole can be seen to be of simple construction.

Apart from the host difference, the main difference seen between *P. fragile* and *P. lejolisii* is the relatively thin tetrasporangia in *P. fragile* (Figs 27A, B) as compared with the normally fat ones of *P. lejolisii*, which usually fill the conceptacle completely.

Distribution: Mediterranean or Yugoslavia (known only from the type specimen). See comments above.

2. **Pneophyllum lejolisii** (Rosanoff) Y. Chamberlain, **comb. nov.**

Basionym: *Melobesia lejolisii* Rosanoff pro parte in *Mém. Soc. Imp. Sci. nat. Cherbourg* **12**: 62, Pl. I, Figs 4, 10, 12 (Fig. 2 of present study), Pl. VII, Figs 9–11 (Fig. 6 of present study), [NOT Pl. I, Figs 8–9 which are probably *Pneophyllum concollum*] (1866).

Nomenclatural synonyms: *Dermatolithon lejolisii* (Rosanoff) Foslie in *K. nor. Vidensk. Selsk. Skr.* **1898** (3): 11 (1898).
Melobesia lejolisii f. *typica* Foslie in *K. nor. Vidensk. Selsk. Skr.* **1905** (3): 102 (1905).
Heteroderma lejolisii (Rosanoff) Foslie in *K. nor. Vidensk. Selsk. Skr.* **1909** (2): 56 (1909).
Fosliella lejolisii (Rosanoff) M. Howe, *In* N. L. Britton and C. F. Millspaugh (Eds), *The Bahama Flora*: 588 (1920).

References: *Melobesia lejolisii* Rosanoff; Areschoug in *Nova Acta reg. Soc. scient. Upsala.* III, **10**: 365, Pl. IX, Fig. 1 (1875); Lemoine in *Annals Inst. Oceanogr. Monaco* **2**: 180 (1911); Rosenvinge in *K. danske*

Vidensk. Selsk. Skr. II, **7**: 238 (1917) (pro parte as to materials, excluding Figs 158D, E which are *Pneophyllum rosanoffii*); Suneson in *Acta Univ. lund.* II, **33**: 7 (1937), in *Acta Univ. lund.* II, **39**: 23 (1943); Hamel and Lemoine in *Archs Mus. natn. Hist. nat. Paris* VII, **1**: 103 (1953 ['1952']), pro parte; Zinova, *Check-list of green, brown and red algae of the southern seas of the U.S.S.R.*: 231 (1967).

Melobesia lejolisii Rosenv. [sic]; Newton, *A handbook of the British seaweeds*: 302 (1931).

Melobesia membranacea sensu Areschoug in *Nova Acta reg. Soc. scient. Upsala* **13**: 289 (1847), *In* J. G. Agardh (Ed.) *Species, genera et ordines algarum*: 112 (1852).

Heteroderma lejolisii (Rosanoff) Foslie; Dawson in *Pacif. Nat.* **2**: 55 (1960).

Fosliella lejolisii (Rosanoff) M. Howe; Feldmann in *Rev. algol.* **11**: 316 (1942 ['1939']); Taylor, *Marine algae of the north eastern coast of North America* – revised edition: 253 (1957); *Marine algae of the eastern tropical and subtropical coasts of North America*: 387 (1960); Masaki in *Mem. Fac. Fish. Hokkaido Univ.* **16**: 23 (1968); Bressan in *Boll. Soc. adriat. Sci. nat.* **59**: 80 (1974); Parke and Dixon in *J. mar. biol. Ass. U.K.* **56**: 534 (1976); Chamberlain in *Br. phycol. J.* **12**: 73 (1977); Rueness, *Norsk algeflora*: 60 (1977); Garbary, *in* D. E. G. Irvine and J. H. Price (Eds) *Modern approaches to the taxonomy of brown and red algae*: 205–222 (1978).

SPECIMENS: *Melobesia membranacea* sensu Lloyd (1886), *Flore de l'ouest de la France,* Ed. 4, no. 339 (CO!).

M. lejolisii, coll. E. M. Holmes exsiccata no. 265, Clacton-on-Sea, Essex, January 1889, on *Zostera* (BM!; E!).

EXCLUDED RECORDS: *Melobesia lejolisii* auct. div.; Johnson and Hensman in *Scient. Proc. r. Dubl. Soc.* II, **9**: 27 (1899); Wuitner in *Ann. Assoc. naturalistes de Levallois-Peret*, 1914–1931, **20**: 58 (1931). (Both = *Pneophyllum rosanoffii.*)

LECTOTYPE: CHE Herb Le Jolis, Areschoug no. 2 (in *Melobesia membranacea* folder) (Fig. 28A).

DIAGNOSIS: Epiphytic species growing on *Zostera* and other sea-grasses with vegetative thallus of epithallium and hypothallium and one or two tall perithallial cells beside the conceptacles; conceptacles flattened or slightly raised, ostiole simple: differing from *P. rosanoffii* in lacking long, free ostiolar filaments; and from *P. limitatum* in having smaller conceptacles and lacking ostiolar funnel.

DESCRIPTION: Small, delicate, rosy or pale pink crusts up to 2 mm diameter (40 mm when epilithic) and *c.* 30 μm deep, usually with wide vegetative border and crowded central conceptacles, *crust cells* in surface view 3·5–11·5 μm long × 6·5–12 μm wide, *epithallial cells* 1·5–3·5 μm long × 3·5–8 μm wide, intrafilament and branch cell *trichocytes* 11–16 μm long × 8·5–13·5 μm wide; conceptacles flat or slightly raised, with uniform roof and all except

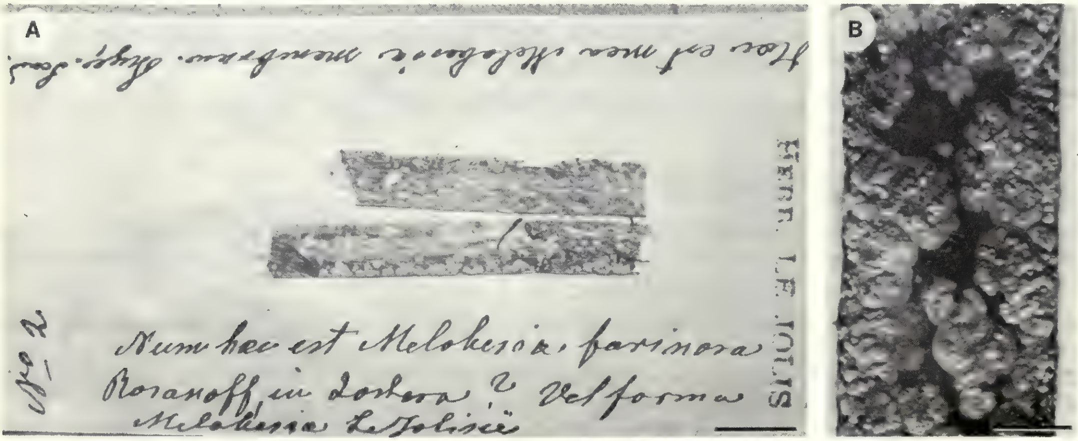

A
B
HERB. LE JOLIS
No 2
Num haec est Melobesia farinosa Rosanoff in Zostera? Vel forma Melobesia Lejolisii

Fig. 28 Type specimen and surface views of *Pneophyllum lejolisii*. A, Lectotype of *Pneophyllum lejolisii* (Rosanoff) Y. Chamberlain, ex Herb. Le Jolis (CHE); specimen sent to Le Jolis by Areschoug. Scale = 10 mm. B, Surface view of *Pneophyllum lejolisii* growing on *Zostera* at Bembridge. Scale = 2 mm.

spermatangial with simple ostiole, *carposporangial conceptacles* 59–91 μm internal diameter × 22–40 μm high, *spermatangial conceptacles* immersed beside carpogonial conceptacles, 13–41 μm wide × 12–21 μm high, ostiole prolonged into a spout, *tetrasporangial conceptacles* 75–125 μm internal diameter × 30–52 μm high, tetrasporangia peripheral, up to 11 per conceptacle, 31–70 μm long × 18–49 μm wide, *bisporangial conceptacles* 91–130 μm internal diameter × 33–65 μm high, bisporangia peripheral, up to 14 per conceptacle, 31–65 μm long × 17–51 μm wide.

HISTORICAL: The name *Melobesia lejolisii* was given by Rosanoff (1866) to simple calcareous crusts from the Cherbourg area growing mainly on *Zostera* but also on *Bornetia secundiflora*. In the course of the present investigation it has become apparent that three taxa were encompassed by Rosanoff's (1866) description of *Melobesia lejolisii* (i.e. *Pneophyllum lejolisii, P. rosanoffii,* and *P. concollum*): because these are all important entities in the northern European species of simple calcareous crusts, the evidence for the decisions made about the identity of the three taxa is discussed in detail on pp. 304–305, and copies of Rosanoff's published plates are included for reference.

Pneophyllum lejolisii, as now defined, is the commonest of the three taxa concerned, and it is the entity to which the epithet *lejolisii* has been almost exclusively applied since Rosanoff's publication. *P. lejolisii* grows predominantly on marine angiosperms and comprises delicate crusts with more or less isodiametric cells, and flat to slightly raised conceptacles with simple ostioles. Weber van Bosse (1886) described material from the Netherlands and illustrated a spermatangial conceptacle; her specimens (L) are typical examples of the taxon. Foslie (1905*a*) described material from Norway and Denmark and distinguished forma *limitata* (see *P. limitatum*); *P. lejolisii* underwent a number of nomenclatural changes in Foslie's publications, as can be seen in the synonymy. Lemoine (1911), Rosenvinge (1917), and Suneson (1937, 1943) described further European material of *P. lejolisii* (all as *Melobesia*) and I made a preliminary study of *P. lejolisii* growing on *Zostera* at Bembridge on the Isle of Wight (Chamberlain, 1977*a*, as *Fosliella*). It is clear from the publications of, for example, Taylor (1957, 1960, as *Fosliella*) from North America, Dawson (1960, as *Heteroderma*) from Pacific Mexico, and Masaki (1968, as *Fosliella*) from Japan that the species has a wide extra-European distribution.

P. lejolisii has been recorded by some authors (e.g. Rosanoff, 1866; Bressan, 1974; Woelkerling, 1975) as growing on algal hosts. However, the sample referred to by Rosanoff as growing on *Bornetia secundiflora* is not *Pneophyllum lejolisii* (see further under *P. concollum*), and I have not been able to examine any other specimen referred to this species growing on an algal host. This is important in respect to the type species, *P. fragile* Kütz., of *Pneophyllum,* and is discussed under that species.

A study of conceptacle type variation is presented in Chamberlain (1982).

The choice of lectotype is discussed on p. 305.

CRUST APPEARANCE: *P. lejolisii* forms thin (up to 30 μm thick) crusts epiphytic on *Zostera marina* (Fig. 28B). The crusts are deep pink in shaded situations, but become pale pink or white under more intense illumination. The crusts rarely exceed 2 mm diameter; early in the season (July–September) they are usually more or less orbicular with a wide, semitransparent border, and centrally situated conceptacles; as the season progresses they become densely crowded and more heavily calcified so that individual crusts are indistinguishable. The crusts adhere fairly well to the host, but can usually be detached without difficulty.

Under the S.E.M. (Fig. 29D) the crust cells appear rather broad, with epithallial concavities broader than long. Intrafilament and branch cell trichocytes occur; these are usually considerably larger than normal crust cells and lack epithallial concavities. Decalcified crusts examined under the S.E.M. show ridge-like cell walls enclosing collapsed cell contents, and the same effect is occasionally seen in very young crusts which suggests that the onset of calcification may sometimes be delayed (Chamberlain, 1982).

The conceptacles vary from being flattened (Fig. 29B) and closely crowded to being rounded, prominent (Fig. 29A), and more widely spaced. The conceptacle roofs are uniform and the

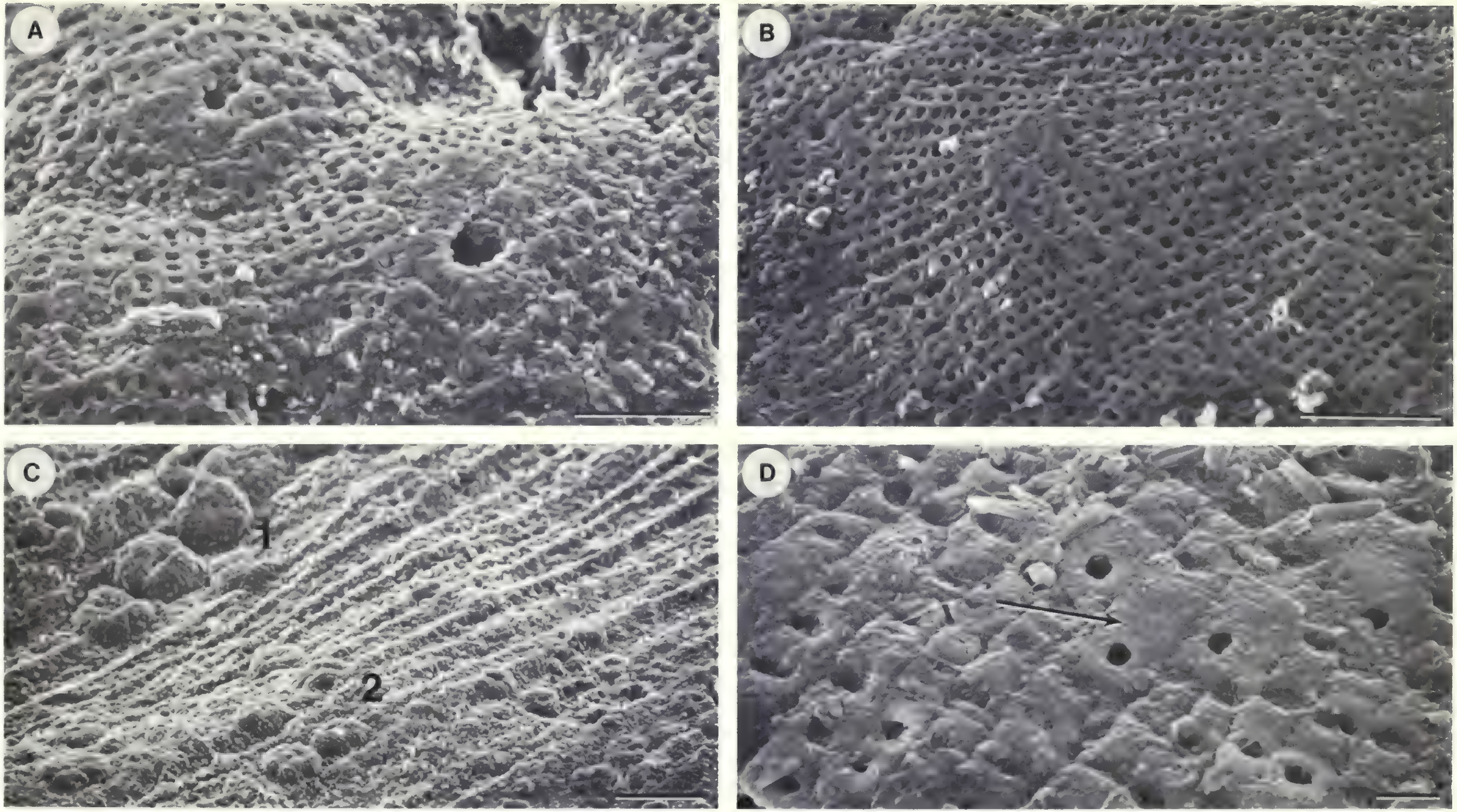


Fig. 29 Scanning electron micrographs to show crust surface features of *Pneophyllum lejolisii*. A, Large type conceptacles. Scale = 50 μm. B, Small, mosaic-type conceptacles. Scale = 50 μm. C, Decalcified crust showing large (1) and small (2) type conceptacles. Scale = 100 μm. D, Crust cells and intercalary trichocytes (arrow). Scale = 10 μm.

simple ostioles are usually surrounded by rosettes of varying numbers of cells, although these may be absent or masked by a surface covering. Decalcified preparations (Fig. 29C) show the same variety of conceptacle size as calcified crusts, but the conceptacles appear dome-like and the cells on their roof become prominent.

On two occasions, in May 1977 and November 1978, *P. lejolisii* was found growing epilithically on pieces of glass and china; the crusts were similar to those found on *Zostera* early in the season, being discrete and with a wide sterile border and crowded central conceptacles, but they grew much larger (up to 40 mm diameter) than epiphytic crusts.

VEGETATIVE ANATOMY: The vegetative thallus of *P. lejolisii* is composed of hypothallium and epithallium with perithallial cells developing only in the neighbourhood of conceptacles; these perithallial cells are tall and thin (Figs 31, 32). However, the crust centre is so crowded with conceptacles that a VS in that area will usually cut through both conceptacle chambers and walls of adjacent conceptacles giving the impression that the thallus is several cells deep (cf. Lemoine, 1911). In surface view the crust cells (Fig. 30G), are typically short and wide, with thick walls which are not heavily calcified; cell fusions are particularly common in this species. The epithallial cells are usually about twice as wide as long. Intrafilament and branch cell trichocytes (Fig. 30G) are very abundant between July and October, mature ones are conspicuously larger than adjacent crust cells and are divided by a radial wall. The very large trichocytes, up to 30 μm long, recorded previously (Chamberlain, 1977*a*) came from more central parts of the crust.

Epilithic plants have similar vegetative cells which measure 8–15 μm long × 8–11 μm wide with short, wide epithallial cells.

GAMETANGIAL PLANTS: The crusts are usually monoecious although crusts bearing only carpogonial conceptacles (Figs 30C, H) are also common. When spermatangial conceptacles are present they are immersed in the thallus adjacent to the carpogonial conceptacles (Figs 30D; 31); they are relatively broad and shallow and the ostiole is prolonged into a spout (Fig. 30F). The structure and development of spermatangial conceptacles are described and illustrated by Suneson (1937), who shows that spermatangia are released at two points on each initial. Suneson (1937) also shows the stages in the development of the carpogonial conceptacles which have quite a small number of procarps on each fertile disc; the central procarps bear one or two carpogonia, and in one case (Suneson, 1937, Fig. 3B) a transfer tube is shown extending from the carpogonium to the auxiliary cell.

As has been discussed in Chamberlain (1982), the carpogonial conceptacles on crusts lacking spermatangia are usually somewhat smaller than when spermatangia are present, and rarely exceed about 65 μm surface diameter.

CARPOSPORANGIAL CONCEPTACLES: Carposporangial conceptacles (Figs 30C, D; 31; 32A) are either entirely flat or somewhat raised, they have a thin roof with slightly developed downward ostiolar filaments, and very short filaments round the ostiole itself which may show as a rosette of wedge-shaped cells in surface view under the S.E.M. The fusion cell is narrow and fairly deep, the gonimoblast filaments are given off peripherally, and may often be seen clearly in the surface view of decalcified crusts (Fig. 30H).

In epilithic crusts, carposporangial conceptacles on crusts without spermatangia measure 60–70 μm internal diameter and those with spermatangia measure 90–110 μm, which is slightly larger than found in epiphytic plants in the present investigation, although other authors (e.g. Taylor, 1957; and Bressan, 1974) have recorded larger diameters. The larger maximum dimensions recorded for carposporangial conceptacles and other structures by Hamel & Lemoine (1953) (Tab. 11) are possibly caused by failure to distinguish *P. rosanoffii* from *P. lejolisii*.

TETRASPORANGIAL PLANTS: Tetrasporangial conceptacles (Figs 30A; 32B) show the same development and structure as carposporangial conceptacles, but are somewhat larger. In Chamberlain (1982) it is shown that they tend to fall into two groups (Fig. 30A) composed of smaller, mosaically-arranged conceptacles, and larger, more spaced out, conceptacles respectively. The

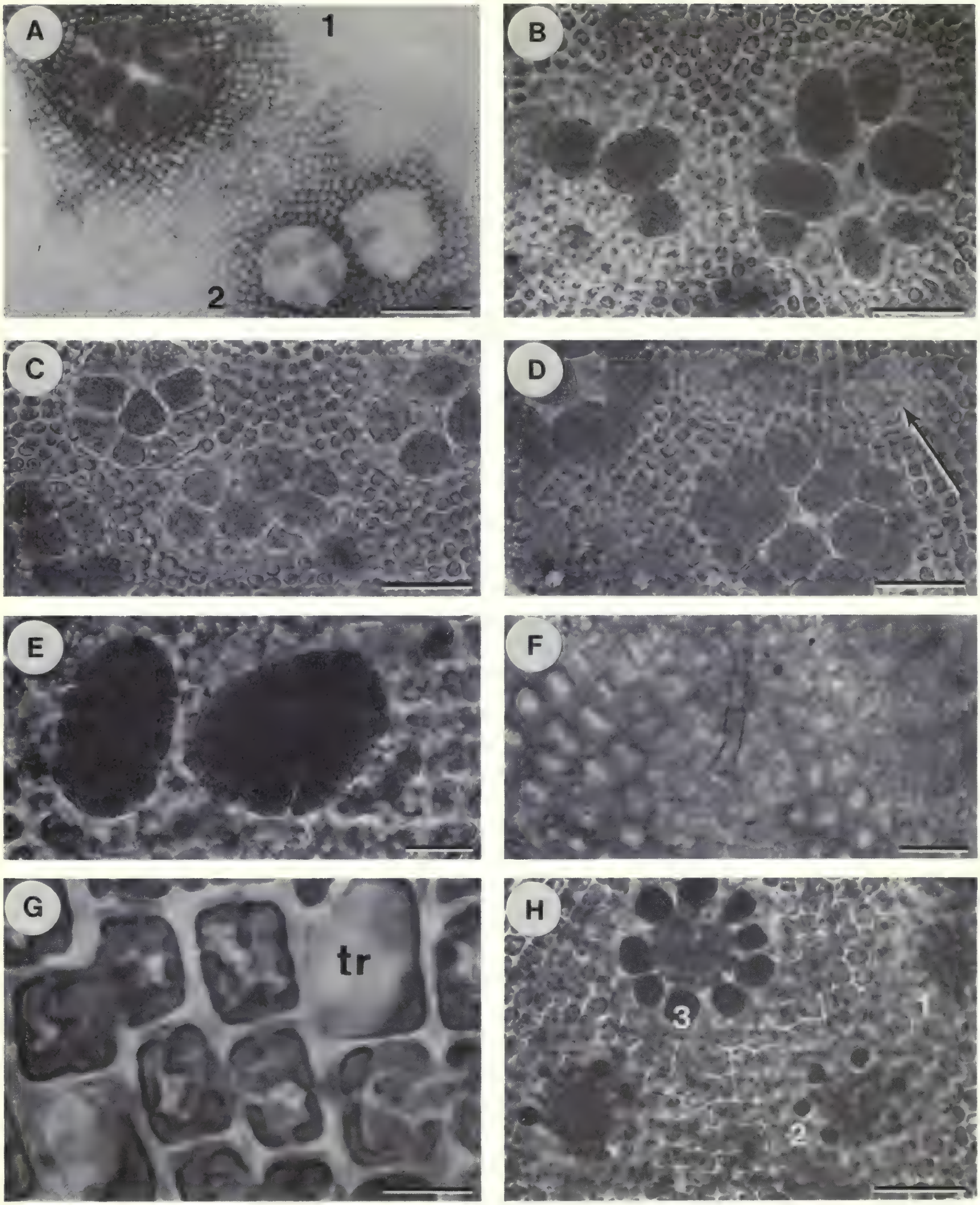


Fig. 30 Surface views of decalcified crusts of *Pneophyllum lejolisii*. A, Large (1) and small (2) type tetrasporangial conceptacles. Scale = 100 μm. B, Bisporangial conceptacles. Scale = 50 μm. C, Small type carposporangial conceptacles. Scale = 50 μm. D, Large type carposporangial conceptacles with spermatangial conceptacles (arrow). Scale = 50 μm. E, Tetrasporangium and bisporangium in same conceptacle. Scale = 20 μm. F, Spout of spermatangial conceptacle. Scale = 20 μm. G, Crust cells with intercalary trichocyte (tr). Scale = 10 μm. H, Gonimoblast filaments at successive stages (1, 2, 3) of development. Scale = 50 μm.

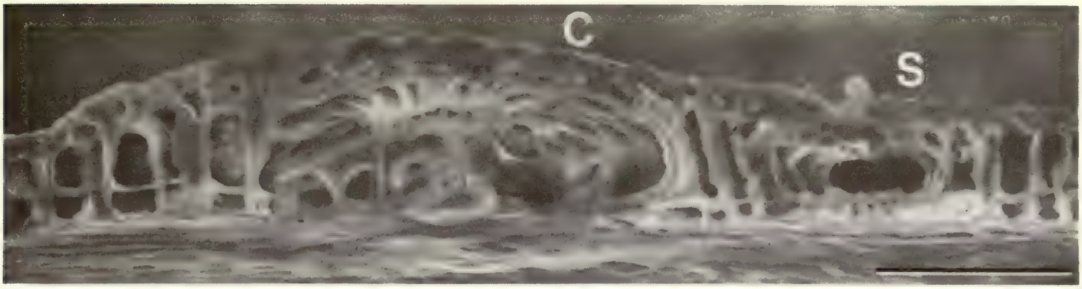


Fig. 31 Scanning electron micrograph of vertical fracture of gametangial crust of *Pneophyllum lejolisii* showing carposporangial (c) and spermatangial (s) conceptacles. Scale = 50 μm.

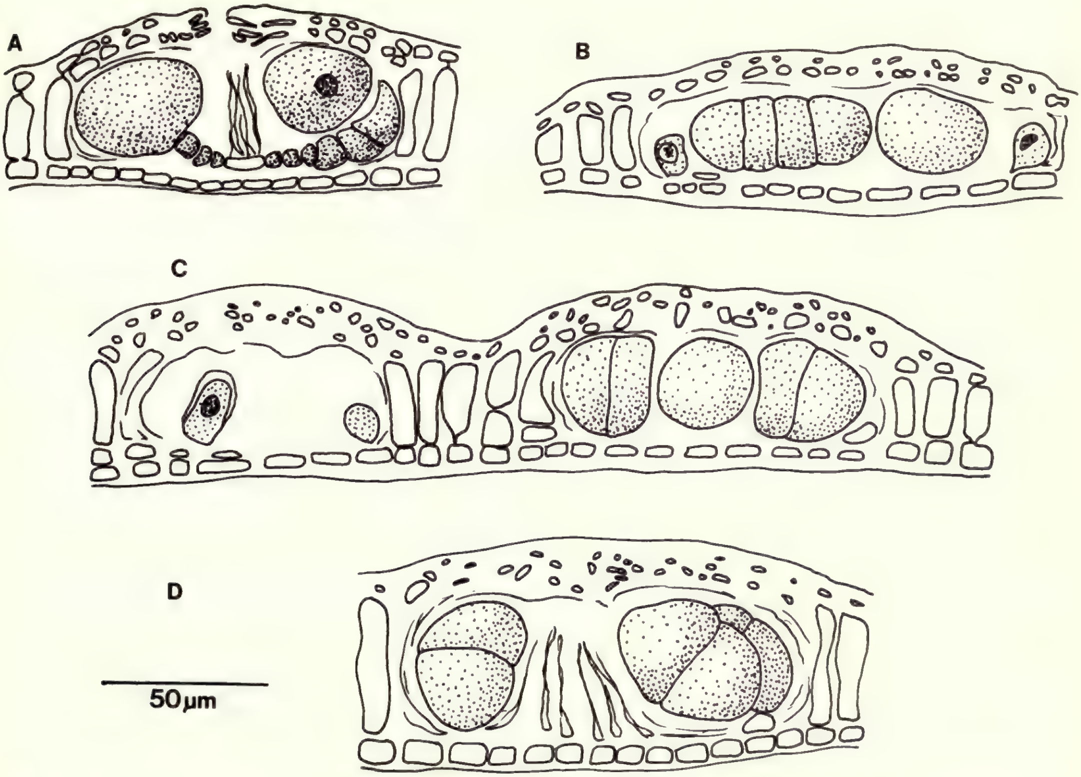


Fig. 32 Vertical sections of *Pneophyllum lejolisii* conceptacles. A, Carposporangial conceptacle. B, Tetrasporangial conceptacle. C, Young and mature bisporangial conceptacles with bisporangia lying horizontally. D, Large bisporangial conceptacle with bisporangia ± vertical.

tetrasporangia are borne peripherally on stalk cells and their development is described and illustrated by Suneson (1937); he shows that central, sterile cells are present in the young conceptacle, but may be absent in mature conceptacles. Mature tetrasporangia are large in relation to the small size of the conceptacle. In epilithic crusts the conceptacles measure 70–80 μm internal diameter, with 5–6 tetrasporangia per conceptacle which measure about 45–50 μm long.

Bisporangial plants: Bisporangial plants are similar to carposporangial and tetrasporangial plants. Bisporangial conceptacles (Figs 30B; 32C, D) are the largest type found in *P. lejolisii* (see Chamberlain, 1982) and show a general gradation in size, with no suggestion of forming two groups as is seen with tetrasporangial and carposporangial conceptacles. The bisporangia are somewhat globular and, like the tetrasporangia, are very large in relation to conceptacle size. In the smaller conceptacles the bisporangia lie horizontally (Fig. 32C), while they are more or less vertical in the larger conceptacles (Fig. 32D). Bisporangia and tetrasporangia are sometimes found in the same conceptacle (Fig. 30E), particularly in the autumn (Chamberlain, 1982).

PHENOLOGY: *P. lejolisii* is the only species of *Pneophyllum* investigated which has a pronounced seasonal cycle of presence and absence. Crusts start to appear on intertidal *Zostera* at Bembridge in July and disappear again between January and April depending on the weather. The only exceptions are the epilithic crusts collected in May which had presumably been cast from the subtidal zone; Rosenvinge's (1917) and Suneson's (1943) results also indicate that crusts appear earlier in the subtidal in Denmark and Sweden since they record their presence in May and June respectively. Reports from other parts of the world show that *P. lejolisii* occurs seasonally elsewhere; van der Ben (1969, as *Melobesia*) records its presence on *Posidonia* in the Mediterranean from January till October, and Brauner (1975, Tab. I, as *Heteroderma*) shows that, while it is present throughout the year except in June on *Zostera marina* in North Carolina, it is relatively scarce from March till May.

Very little difference was seen within populations in the relative abundance of different conceptacle types throughout the season, although bisporangial conceptacles increased in number slightly at two sites at Bembridge as the season progressed (Chamberlain, 1982). There was, however, a sharp difference in the proportion of conceptacle types at different sites at Bembridge, with two populations having mainly tetrasporangial and carposporangial conceptacles and a third site predominantly bisporangial conceptacles. This difference was maintained throughout three successive seasons.

FORM RANGE: As remarked by Suneson (1943) and by Bressan *et al.* (1977), *P. lejolisii* shows much variation even at one locality and like these authors, I have found considerable differences in crust cell size both within and between populations. The dimensions given for crust cell size in Table 10 were made on material from Ireland and England collected in August and September, which is probably the optimum season for growth and reproduction. Cells from material collected in November at Bembridge, however, are relatively longer and thinner and measure (7) 11 (16) μm long × (5) 8 (13) μm wide; in addition trichocytes are abundant under warm, well-illuminated conditions, but disappear as winter progresses.

As has been discussed, there is a very considerable range of form and size within each conceptacle type and differences are seen in other areas. Masaki (1968, as *Fosliella*), for example, describes the conceptacles of Japanese samples as being convex or hemispherical.

DISTRIBUTION:
British Isles: Northumberland, Essex, Hampshire, Dorset, Devon, Cornwall, Anglesey, Ayrshire, Orkney, Jersey, Co. Clare, Co. Cork.
World: Norway, Sweden, Denmark, Netherlands, France (north and Mediterranean), Italy, Corsica, Canary Islands, Canada, U.S.A. (east and west coasts), Caribbean, Pacific Mexico, Japan, southern U.S.S.R., Australia.

HABITAT: As has been discussed, *P. lejolisii* occurs predominantly as an epiphyte on *Zostera* and other sea-grasses; during the present study it has been found twice growing epilithically on glass and china. Records of its occurrence as an epiphyte on algae require confirmation.

During the present investigation, detailed study (Chamberlain, 1982) has been restricted to crusts growing on *Zostera marina* from the intertidal zone. Here the *Zostera* clumps have either been situated in pools or runs which never dry out completely at low tide since, in common with all other *Pneophyllum* species examined, *P. lejolisii* cannot withstand desiccation. For this reason, it is also more common on *Zostera* blades growing at the edge of clumps than on those on the surface which are more likely to dry out. *P. lejolisii* also grows on subtidal angiosperms in the British Isles and elsewhere (e.g. Weber van Bosse, 1886, Netherlands; van der Ben, 1969, Mediterranean).

At Bembridge, *P. limitatum* occurs with *P. lejolisii* on *Zostera*, but is very much less abundant and mostly recorded early in the season, occasional crusts of *Fosliella farinosa* have also been found. In localities such as Falmouth in the west of England, *Pneophyllum rosanoffii* may grow with *P. lejolisii* on *Zostera*, while in Ireland the two species seem to be equally common, growing either together or in pure stands.

The occurrence of *Pneophyllum lejolisii* in northern Europe suffered a check in the 1930s when a wasting disease destroyed many of the *Zostera* populations (Tutin, 1938). However, in Sweden the epiphyte apparently became plentiful again as soon as the *Zostera* started to recover (Suneson, 1943), and Davey's (1943) record from Wales indicates that this had probably also occurred in the British Isles.

Table 10 Dimensions of vegetative structures (in μm unless stated).

Pneophyllum lejolisii		British Isles	Hamel & Lemoine (1953)	Suneson (1943)	Masaki (1968)
crust diameter		up to 2 mm	0·5 mm		2–4 mm
crust depth		*c.* 30			
crust cell	length	(3·5) 7·5 (11·5)	6–9 (15)	(6) 8–15	8–13
surface	width	(6·5) 9 (12)	6–10	(5) 6–10	5–10
crust cell	height	*c.* 15	7–11		7–11
epithallial cell	length	(1·5) 2·5 (3·5)			2–3
surface view	width	(3·5) 5·5 (8)			3–7
epithallial cell	height				4–5
hypothallial cell	width				
VS	height				
perithallial	width		7–10		6–7
cell	height		17–20		7–20
VS	number				
trichocyte type		mainly intrafilament	intrafilament and branch cell	intrafilament and branch cell	
trichocyte	length	(11) 13 (16)	13	11–16	10–12
surface view	width	(8·5) 10 (13·5)		6–10	6

3. Pneophyllum rosanoffii Y. Chamberlain, sp. nov.

References: *Melobesia farinosa auct. div.*, Le Jolis, *Liste des algues marines de Cherbourg*: 150 (1863); Kützing, *Tabulae phycologicae*: 34 Tab. 95c, d (1869).

Melobesia lejolisii Rosanoff *pro parte* in *Mem. Soc. imp. Sci. nat. Cherbourg* **12**: 62 Pl. I, Figs 1–3, 5–7, 11 (Fig. 2 of present study) (1866).

Melobesia lejolisii auct. div.; Johnson & Hensman in *Scient. Proc. r. Dubl. Soc.* II, **9**: 27 (1899); Rosenvinge in *K. danske Vidensk. Selsk. Skr.* II, **7**: Figs 158D, E only (1917); Mazza, *Saggio di algologia oceanica* **3**: 1116 pro parte (1922); Wuitner in *Ann. Assoc. naturalistes de Levallois-Peret* **20**: 58 (1931).

Specimens: *Pneophyllum fragile* Kütz.; Herb. Kützing (L no. 941.241.153!), on *Zostera* from Adriatic, mixed with other species.

Melobesia lejolisii; Herb. Rosenvinge (C!), no. 6246, Sanden, Denmark, 5 July 1895, on *Zostera*.

Holotype: CHE! Herb. Le Jolis no. 1200, 31 December 1857, Cherbourg, growing on *Zostera marina*! (It is to be found in Le Jolis's *Melobesia lejolisii* folder and is illustrated in Fig. 33). Duplicates of no. 1200 have also been labelled Le Jolis 283 (CHE!), but were apparently never distributed.

Diagnosis: Species epiphytica perithallio prope conceptacula profunditate usque ad 5 cellulas et filamentis ostiolaribus longis liberisque; a *P. sargassi, P. lejolisii, P. limitato* et *P. concollum* filamentis ostiolaribus liberis, et a *P. zonali* crusta tenuiore et conceptaculis minoribus differt.

Descriptio: Crustae laeves, roseae ad pallido roseae, diametro usque ad 4 mm, profunditate 50 μm, perithallium prope conceptacula profunditate usque ad 4 cellulas, *cellulae perithallii* (in sectione verticali) 9–18 μm latae, 12·5–29 μm altae, crusta vegetativa ex hypothallio et epithallio modo constata,

Table 11 Dimensions of reproductive structures (μm unless stated).

Pneophyllum lejolisii	British Isles	Hamel & Lemoine (1953)	Suneson (1937, 1943)	Masaki (1968)
CARPOSPORANGIAL CONCEPTACLE				
external diameter surface diameter	(35) 77 (99)	100–175		
VS internal diameter	(59) 70 (91)		60–100	60–80
VS height	(22) 34 (40)	35–60	30–60	(25) 38–50
VS roof height	(6) 8 (9)			10–13
roof type	uniform			
no. basal cell rows	1	1	1	1
ostiole	simple	simple	simple	simple
no. gonimoblast filaments	5–16		*c.* 6	
diameter carpospore	(20) 26 (32)			
SPERMATANGIAL CONCEPTACLE				
VS/surface width	(13) 34 (41)	40–55	40–55	21–33
VS height	(12) 16 (21)			21–33
length spermatium	3–4			2–4
width spermatium	1·5–2			1
TETRASPORANGIAL CONCEPTACLE				
external diameter surface diameter	(52) 102 (135)			
VS internal diameter	(75) 92 (125)	(90) 125–200 (250)	65–130	75–100 (120)
VS height	(30 42 (52)	45–80	40–90	(24) 43–63
VS roof height	(6) 9 (13)			10–13
roof type	uniform			
no. basal cell rows	1	1	1	1
ostiole	simple	simple	simple	simple
no. tetrasporangia	4–11	1–10	1–10 (20)	
length tetrasporangium	(31) 50 (70)	45–80		(25) 30–50
width tetrasporangium	(18) 33 (49)	30–50		(13) 23–30 (48)
BISPORANGIAL CONCEPTACLE				
external diameter surface diameter	(70) 114 (140)			
VS internal diameter	(91) 101 (130)		65–130	
VS height	(33) 49 (65)		40–90	
VS roof height	(7) 10 (13)			
roof type	uniform			
no. basal cell rows	1		1	
ostiole	simple		simple	
no. bisporangia	3–14		5–20	
length bisporangium	(31) 51 (65)			
width bisporangium	(17) 35 (52)			

cellulae crustae aspectu superficiali rectangulares, 5·5–15·5 μm longae × 4·5–10·5 μm latae, *cellulae epithallii* 2–5 μm longae × 2–9·5 μm latae, *trichocyti* et intra filamenta et ramos facientes frequentes, amplitudine eadem ac cellularum crustae; conceptacula, praeter ea spermatangialia, prominentia, ostiola in statu vivo nitentia, filamentis ostiolaribus longis liberis circumcincta, *conceptacula carposporangialia* diametro interno 84–156 μm, altitudine 45–117 μm, *conceptacula spermatangialia* immersa, 25–50 μm lata × 19–46 μm alta, ostiolo in canalem producto, *conceptacula tetrasporangialia* diametro interno 104–164 μm, altitudine 70–164 μm, usque ad 20 tetrasporangiis in unoquoque conceptaculo, tetrasporangia 41·5–78 μm longa × 26–45·5 μm lata.

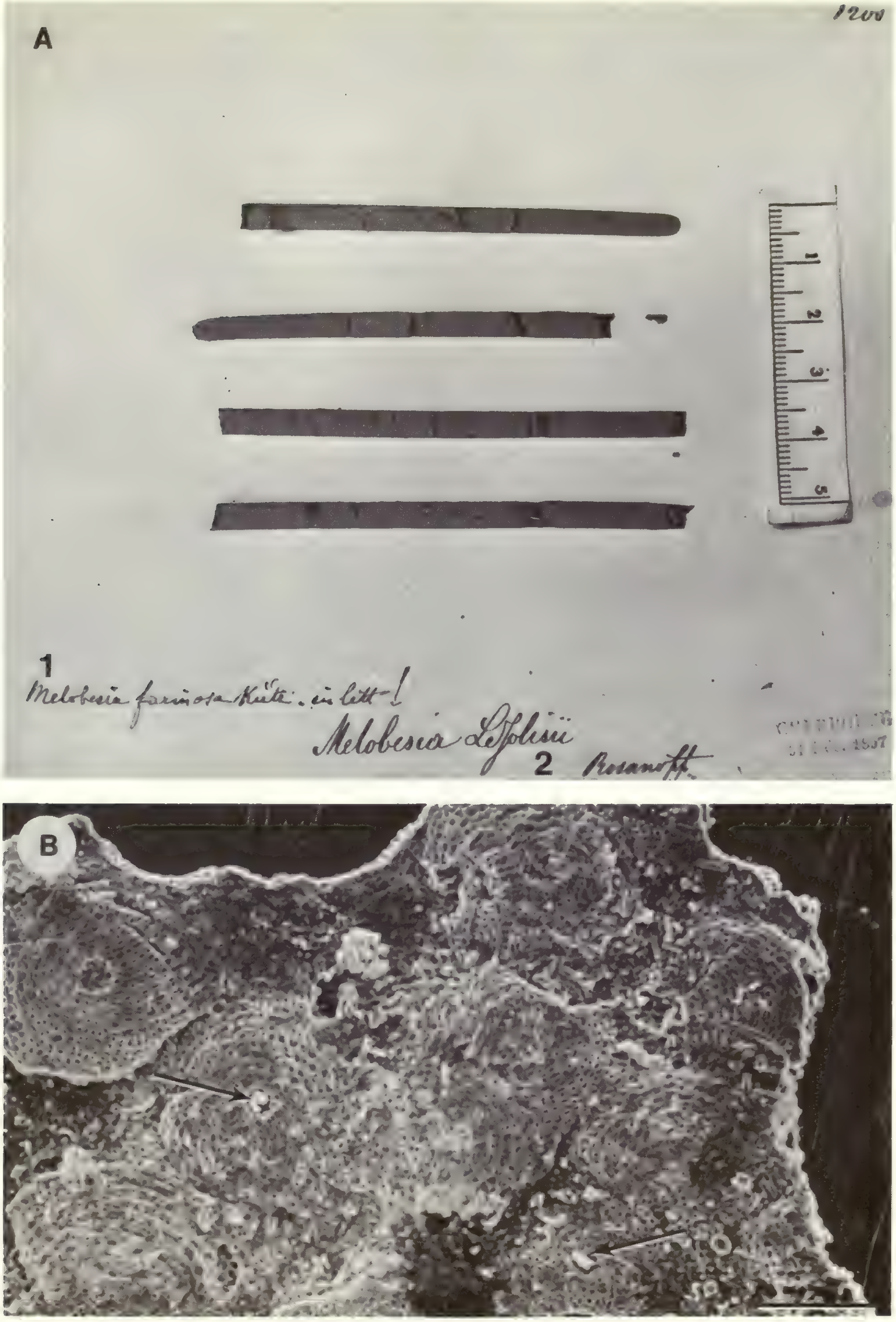

A
1200
1
2
3
4
5
1
Melobesia farinosa Kütz. in litt.!
Melobesia Lejolisii
2
Rosanoff
B

Fig. 33 Type specimen of *Pneophyllum rosanoffii* (= *Melobesia lejolisii* Rosanoff *pro parte*). A, *Melobesia lejolisii*, Le Jolis No. 1200, Herb. Le Jolis, Cherbourg; Rosanoff's handwriting (1), Le Jolis's handwriting (2). B, Scanning electron micrograph of crusts from A; ostiole filaments indicated by arrows. Scale = 100 μm.

DIAGNOSIS: Epiphytic species with perithallium near conceptacles up to 5 cells deep and long, free ostiolar filaments: differing from *P. sargassi, P. lejolisii, P. limitatum*, and *P. concollum* in having free ostiolar filaments, from *P. zonale* in having a thinner crust and smaller conceptacles.

DESCRIPTION: Crusts deep to pale pink, smooth, up to 4 mm diameter, 50 μm deep, perithallium up to 5 cells deep near conceptacles, *perithallial cells* (in VS) 9–18 μm wide × 12·5–29 μm high; vegetative crust of hypothallium and epithallium only, *crust cells* in surface view rectangular, 5·5–15·5 μm long × 4·5–10·5 μm wide, *epithallial cells* 2–5 μm long × 2–9·5 μm wide, intrafilament and branch cell *trichocytes* common, of same size as crust cells; conceptacles (except spermatangial) raised, ostiole shiny when living, surrounded by long, free ostiolar filaments, *carposporangial conceptacles* 84–156 μm internal diameter × 45–117 μm high, *spermatangial conceptacles* immersed, 25–50 μm wide × 19–46 μm high, ostiole prolonged into a spout, *tetrasporangial conceptacles* 104–164 μm internal diameter × 70–164 μm high, up to 20 tetrasporangia per conceptacle, 41·5–78 μm long × 26–45·5 μm wide.

HISTORICAL: This taxon was first described by Le Jolis (1863, p. 150) as *Melobesia farinosa* growing on *Zostera*, having flattened conceptacles with ostioles surrounded by hairs. Le Jolis published it as *Melobesia farinosa* because he had sent some of the material to Kützing who had identified it as this species. The collection on which Le Jolis's description was based was 'A Le Jolis, no. 1200, Cherbourg, 31 Décèmbre 1857' (Fig. 33). Several samples from this collection are in Herb. Le Jolis (CHE) and the sample sent to Kützing is in Leiden, no. 941.156.75; all have been examined during the present investigation. The species was illustrated by Kützing (as *Melobesia farinosa*) in Tabulae Phycologicae (Kützing, 1869, p. 34, Tab. 95c, d).

Rosanoff (1866: 62) considered that the entity differed from *M. farinosa* and described a new species *M. lejolisii*, based partly on this material. As discussed on p. 305 however, three distinct components were included in *Melobesia lejolisii* Rosanoff, and as one of these (the entity with flat-topped conceptacles lacking ostiolar filaments) has come to be widely accepted as *lejolisii*, it seems preferable to continue to apply the epithet to this entity and give a new name to the present species. The name *rosanoffii* has been chosen to commemorate the author of the first detailed description of the species.

Although this appears to be a common European alga, the only records (since Rosanoff's) of its occurrence which have been traced are those of Johnson & Hensman (1899: 27) from Ireland, Rosenvinge (1917, Fig. 158D, E only) from Denmark, Mazza (1922) from Italy, and Wuitner (1931) from France (all as *M. lejolisii*).

Further discussion of Rosanoff's original description is given on p. 304. Le Jolis's specimen no. 1200 is chosen as the holotype and the species description is based on this material, together with British material. Information is also given (Tab. 12) about material gathered from Roscoff (Brittany) in order to gain further insight into the variation of *Pneophyllum rosanoffii* in France.

CRUST APPEARANCE: *P. rosanoffii* forms rather thin crusts (up to 50 μm deep) which grow epiphytically on *Halopitys incurvus, Palmaria palmata,* and *Zostera marina*. When fresh, crusts are a somewhat translucent brownish pink, while dried crusts appear solid and bright rosy pink to brownish or greyish pink depending on the conditions under which they had been growing. The crusts measure up to about 4 mm diameter. They adhere firmly to *Palmaria* and *Zostera*, but on dried *Halopitys* they maintain their rigidity as the host plant shrinks, so that they are liable to flake off or form a sleeve encircling the host but becoming detached. The somewhat raised conceptacles are easily distinguished in fresh material by having a conspicuously shiny ostiole.

Under the S.E.M. (Fig. 34B) the crust cells are rectangular with conspicuous epithallial concavities; branch cell and intrafilament (Fig. 34B) trichocytes are present and bear epithallial concavities. The tetra- and carposporangial conceptacles are somewhat raised, they have uniform roofs and long ostiolar filaments which are clearly visible in mature crusts (Fig. 34A); it is these that impart the characteristically shiny appearance to the ostiole in fresh material. Figures 34C-E show the development of the ostiolar filaments in air dried material, while Figure

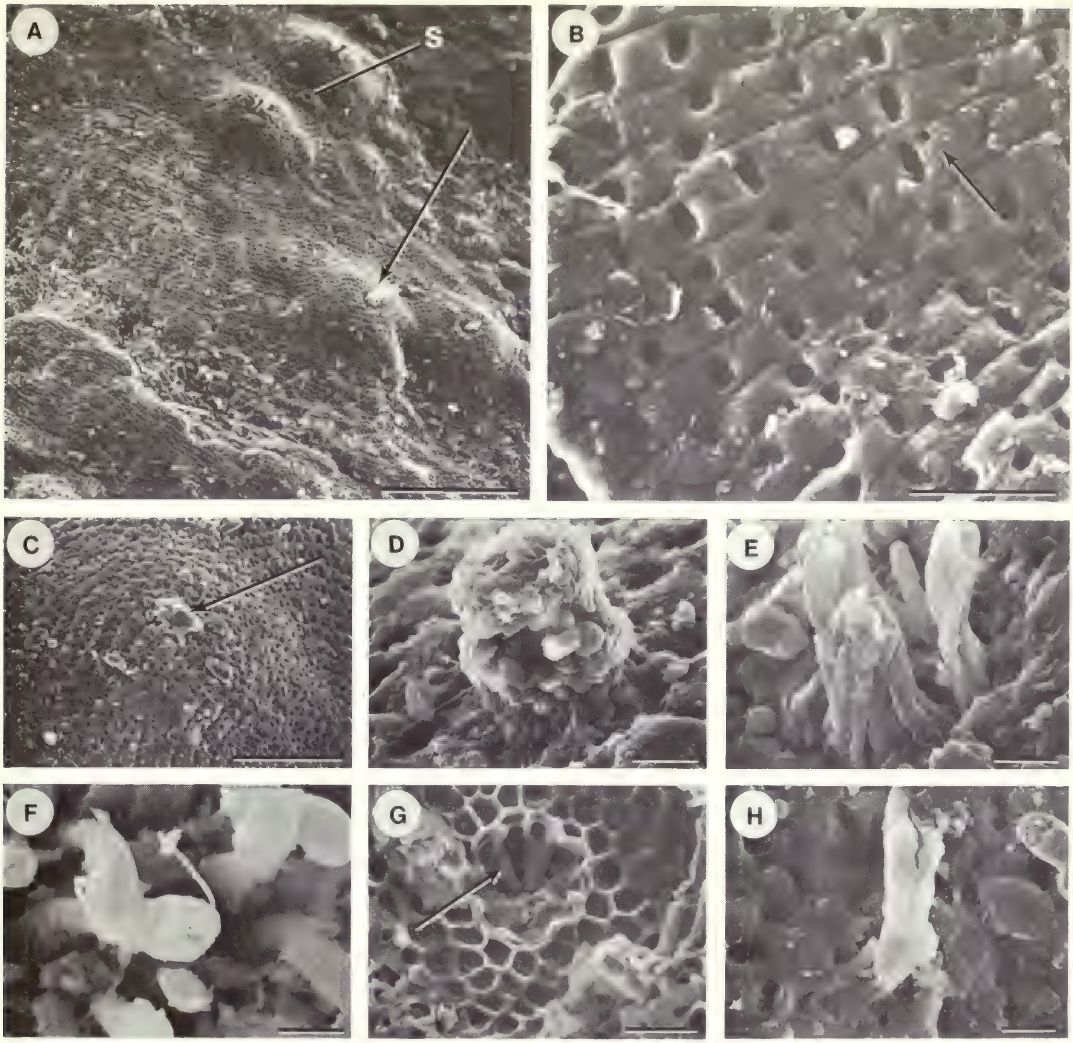


Fig. 34 Scanning electron micrographs of *Pneophyllum rosanoffii*. A, View of critical point dried crust surface showing spermatangial (s) ostioles and carposporangial conceptacles with ostiole filaments (arrow). Scale = 250 μm. B, Critical point dried crust cells with intercalary trichocyte (arrow). Scale = 25 μm. C–E, Stages in the development of ostiole filaments. C, Ostiole filaments starting to emerge (arrow). Scale = 100 μm. D, Ostiole filaments emergent but still fused. Scale = 10 μm. E, Ostiole filaments free. Scale = 10 μm. F, Critical point dried ostiole filaments from above, showing their terete structure. Scale = 5 μm. G, View looking up into the conceptacle roof showing the basal parts of ostiole filaments (arrow). Scale = 25 μm. H, Spermatangial conceptacle with spout. Scale = 10 μm.

34F shows the terete nature of the filaments in critical point dried material. Spermatangial conceptacles (Figs 34A, H) can be seen beside the carposporangial conceptacles.

VEGETATIVE ANATOMY: The vegetative crust is composed of epithallium and hypothallium only. In surface view the crust cells (Fig. 35A) are robust, rectangular, and particularly well pigmented, and the epithallial cells are conspicuous and rectangular; the germination disc is sometimes visible in mature crusts. Intrafilament trichocytes occur quite commonly; they appear always to bear epithallial cells. In Irish and Roscoff material both intrafilament and branch cell trichocytes are present and may bear long hairs. Trichocytes on British material are of a similar size to the surrounding crust cells, but those in the Irish and Roscoff material are noticeably longer. A perithallium up to five cells deep develops in the region of the conceptacles, the cells vary from square to vertically elongated in vertical section (Figs 12A–H).

GAMETANGIAL PLANTS: The crusts are monoecious with spermatangial conceptacles adjacent to carpogonial conceptacles (Figs 34A; 36C). The spermatangial conceptacles are small, immersed, flask-like chambers and the ostiole is prolonged into a spout (Figs 12H; 34H). The carpogonial conceptacles (Fig. 36A) are shallow and wide; their development (Figs 12A–C) follows the normal pattern and the fertile procarps (Fig. 12C) bear one or, more rarely, two carpogonia, with long trichogynes.

CARPOSPORANGIAL CONCEPTACLES: The stages in the development of carposporangial conceptacles are shown in Figures 12E–G and 36B. The conceptacles of *P. rosanoffii* are neat and regularly symmetrical. The roof is composed of a single, rather regular layer of cells each with an epithallial cell; it is gently rounded (Figs 34A; 36B) and has a uniform upper surface. The downward ostiole filaments are quite well developed, whilst the upper filaments are prolonged into a corona of tentacle-like filaments (e.g. Figs 12F; 36B) which are about 50 μm long when mature. This is very characteristic of the species, it is important, however, to appreciate that young and senescent plants may not necessarily show this feature. The filaments can also be seen in whole crust mounts by focusing up in the ostiole area (Fig. 35B) while their basal parts are visible in the conceptable roof under the S.E.M. (Fig. 34G). The fusion cell (Figs 12E, F) is quite broad, and the peripheral carposporangial filaments are composed of small cells, while the carposporangium is relatively large.

TETRASPORANGIAL PLANTS: Tetrasporangial conceptacles are similar in structure and development to carposporangial ones. The tetrasporangia are borne peripherally on stalk cells and the centre of the conceptacle is occupied by a columella of sterile cells. The young tetrasporangia are pale, thread-like and deeply invaginated zonately into four (Fig. 37A); they are contained in a loose, balloon-like, hyaline sac. The tetrasporangium swells and becomes pigmented, remaining deeply invaginated (Figs 37B, E) and four nuclei can often be seen at this stage. Before final maturation, however, the sporangium swells and apparently loses its divisions (Fig. 37C); it subsequently redivides zonately into four cells and rounds off to become the characteristic farctate tetrasporangium (Figs 37E, F). Mature conceptacles in surface view (Fig. 37F) show the tetrasporangia to be numerous and markedly peripheral. On one occasion, a bisporangium (Fig. 37D) was seen in an otherwise tetrasporangial crust.

BISPORANGIAL PLANTS: Unknown.

PHENOLOGY: *P. rosanoffii* occurs throughout the year on *Halopitys* at Bembridge and Beer, but is most abundant during autumn and early winter. Only sporadic records are available as regards its occurrence on *Zostera*; it will be interesting to know whether it occurs throughout the year on this host, or is absent for a season as with *P. lejolisii*, for example.

FORM RANGE: Regular, rather thin, crusts are typical of *P. rosanoffii* growing under optimum conditions. Under unfavourable conditions (e.g. on *Palmaria* at Beer in a particularly cold winter) the crusts become much thicker and reproduce more slowly. Trichocytes occur during warmer, long day-length seasons of the year. In England only intrafilament trichocytes have been observed; they are quite frequent and are about the same size as surrounding crust cells. In Brittany and Ireland intrafilament and branch-cell trichocytes occur abundantly and are appreciably larger than the crust cells. Material from Brittany is generally larger than English material, while the Irish samples have somewhat shorter crust cells than English specimens (see Tabs 12; 13).

DISTRIBUTION:
British Isles: Hampshire, Dorset, Devon, Cornwall, Jersey, Co. Galway, Co. Clare.
World: Denmark, France (Channel, Atlantic and Mediterranean coasts), North Africa, Italy.

Although this is a newly recognised species, by searching through BM herbarium material of

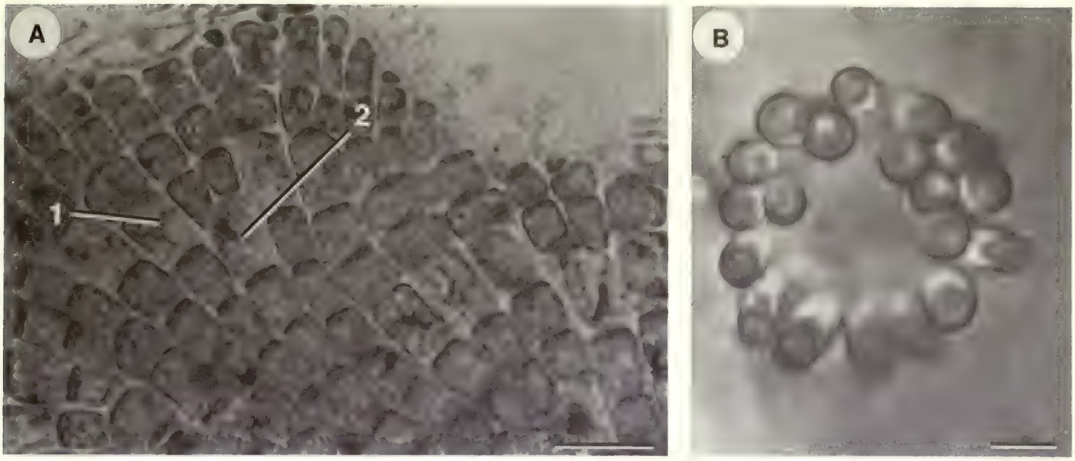


Fig. 35 Decalcified crusts of *Pneophyllum rosanoffii*. A, Crust cells with intrafilament (1) and branch-cell (2) trichocytes. Scale = 20 μm. B, View of ostiolar filaments from above. Scale = 10 μm.

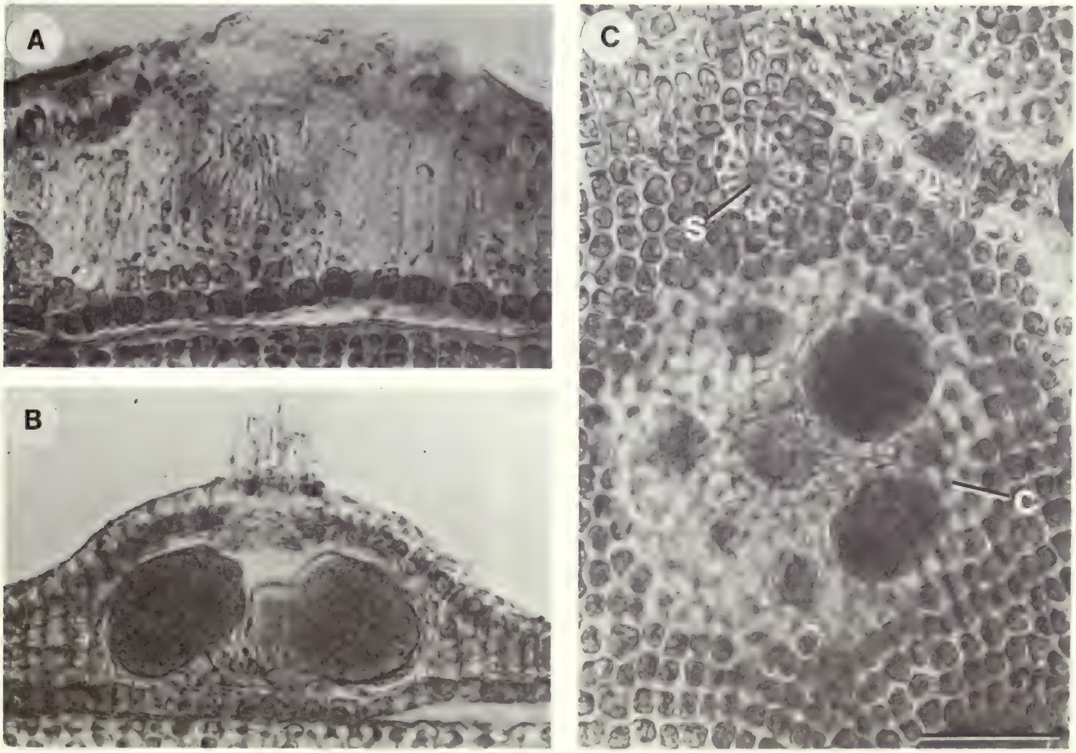


Fig. 36 Gametangial/carposporangial crusts of *Pneophyllum rosanoffii*. A, Vertical section of carpogonial conceptacle. B, Vertical section of carposporangial conceptacle. C, Surface view of young carposporangial (c) and spermatangial (s) conceptacle. Scale = 50 μm (all figures).

one of its characteristic hosts, *Halopitys incurvus*, it has been possible to elucidate the distribution of the epiphyte. By this means it has been found to be common throughout the Mediterranean. It also occurs on *Zostera marina* in the Mediterranean according to Mazza's (1922) description (as *Melobesia lejolisii*), and a specimen of *Zostera* in Kützing's herbarium labelled *Pneophyllum fragile* (L no. 941.241.153) bears *P. rosanoffii* among other species.

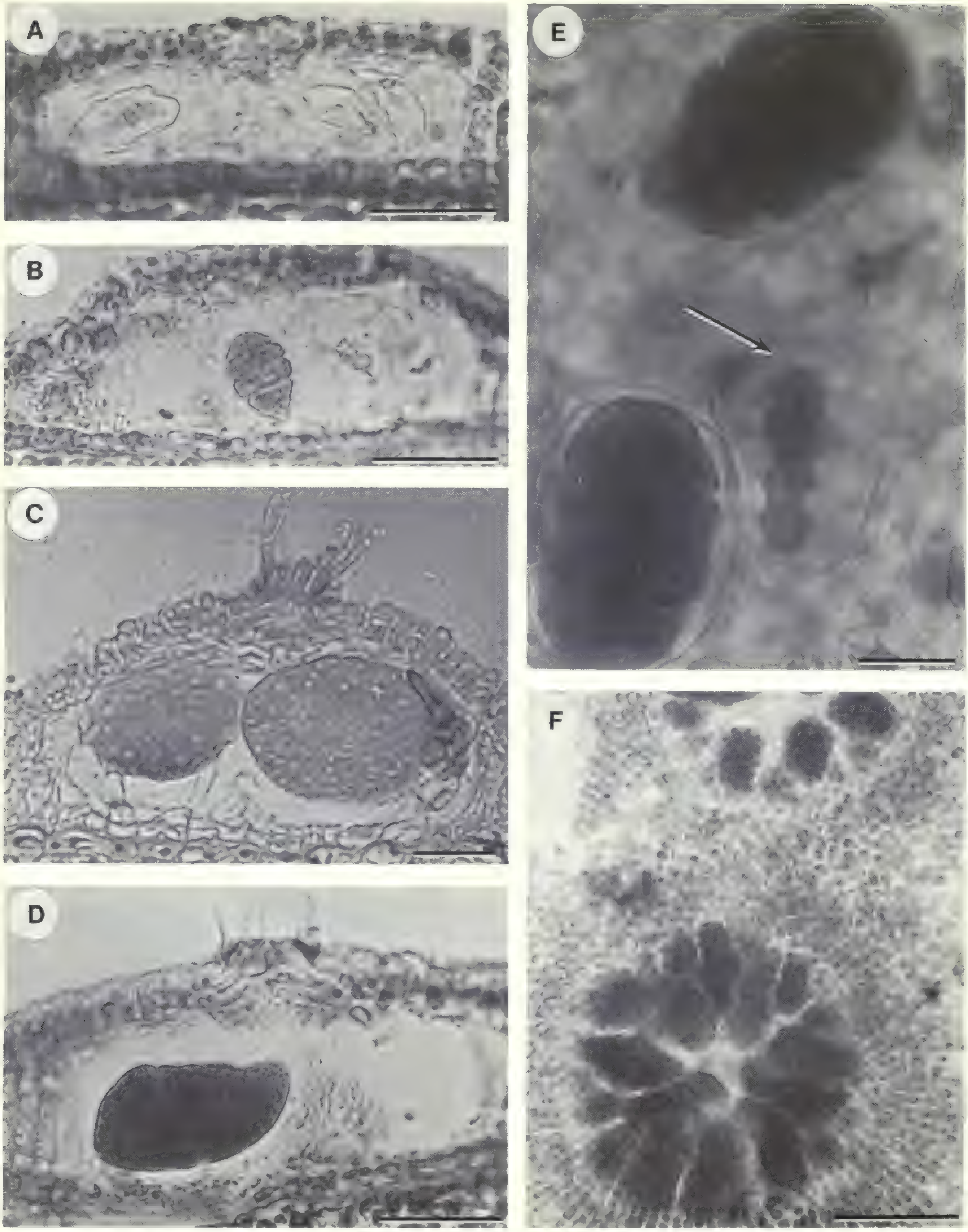


Fig. 37 Sporangial conceptacles of *Pneophyllum rosanoffii*. A, Vertical section of young tetrasporangia in hyaline sacs. Scale = 50 μm. B, Vertical section of immature tetrasporangium. Scale = 50 μm. C, Vertical section of nearly mature tetrasporangial conceptacle in which the zonate divisions have become inconspicuous. Scale = 25 μm. D, Vertical section of bisporangium from an otherwise tetrasporangial crust. Scale = 50 μm. E, Surface view of immature (arrow) and mature tetrasporangia. Scale = 20 μm. F, Surface view of tetrasporangial conceptacles. Scale = 100 μm.

Table 12 Dimensions of vegetative structures (in μm unless stated).

Pneophyllum rosanoffii		England	Ireland	Brittany
crust diameter		up to 4 mm		
crust depth		up to 50		
crust cell	length	(5·5) 11·5 (15·5)	(8) 9·5 (11·5)	(7·5) 12 (15)
surface	width	(4·5) 7·5 (10·5)	(6) 8 (11·5)	(6) 8·5 (11)
crust cell	height	(7) 11 (16)		
epithallial cell	length	(2) 3·5 (5)	(1·5) 3 (4·5)	(3) 4·5 (6·5)
surface view	width	(2) 5·5 (9·5)	(4) 5·5 (7·5)	(3·5) 7·5 (8)
epithallial cell	height	3–6		4–9
hypothallial cell	width			
VS	height			
perithallial	width	(9) 12 (18)		(10·5) 13 (18)
cell	height	(12·5) 20 (29)		(10·5) 17·5 (27)
VS	number	1–5		1–4
trichocyte type		intrafilament	intrafilament and branch cell	intrafilament and branch cell
trichocyte	length	as crust cells	(12·5) 14 (7·5)	
surface view	width	as crust cells	(8·5) 9·5 (10·5)	

RIDGWAY COLOUR CODE: dry crust – light grayish vinaceous, pl. XXXIX

Table 13 Dimensions of reproductive structures (μm unless stated).

Pneophyllum rosanoffii	England	Le Jolis no. 1200
CARPOSPORANGIAL CONCEPTACLE		
external diameter		
surface diameter	(110) 137 (170)	90–130
VS internal diameter	(84) 110 (156)	*c.* 80
VS height	(45) 78 (117)	
VS roof height	(13) 28 (52)	
roof type	uniform	
no. basal cell rows	1–3	
ostiole	long terete filaments	
no. gonimoblast filaments	up to 12	
diameter carpospore		
SPERMATANGIAL CONCEPTACLE		
VS/surface width	(25) 39 (50)	*c.* 30
VS height	(19) 36 (46)	
length spermatium	3·5–5·5	
width spermatium	2–3	
TETRASPORANGIAL CONCEPTACLE		
external diameter		
surface diameter	(104) 147 (182)	155–170
VS internal diameter	(104) 138 (164)	122
VS height	(70) 109 (164)	50
VS roof height	(13) 32 (57)	15·6
roof type	uniform	uniform
no. basal cell rows	1–2	
ostiole	long terete filaments	
no. tetrasporangia	up to 20	
length tetrasporangium	(41·5) 62 (78)	35–45
width tetrasporangium	(26) 40 (45·5)	26–35

This is almost certainly one of the most common European species of *Pneophyllum,* and now that it has been separated from *P. lejolisii*, it should be easy to identify because of the very characteristic ostiolar filaments which can readily be seen in both fresh and dried material. It seems probable that southern Britain and Denmark are its northern limits of distribution.

HABITAT: In the British Isles, *P. rosanoffii* occurs most frequently on intertidal plants of *Halopitys incurvus* along the south coast of England and in the Channel Islands. It usually grows in association with *Melobesia membranacea* and *Pneophyllum sargassi*. It also grows occasionally on *Palmaria* and *Zostera* in the inter- and subtidal zones. At Beer (Fig. 18) it forms a regular association with *Pneophyllum concollum* on intertidal *Palmaria palmata* between about October and April.

In Ireland *P. rosanoffii* occurs commonly on *Zostera* in the inter- and subtidal zones, often growing together with *P. lejolisii*.

In France *P. rosanoffii* appears to be common on *Zostera* and *Halopitys* in Normandy, and is probably very abundant on *Zostera* in Brittany.

It is curious that, although *P. rosanoffii* grows so commonly on *Zostera* in France and Ireland and is also found on this host in Devon and Cornwall, it has never been found during extensive investigations on *Zostera* growing at Bembridge, despite its abundance on *Halopitys* at this locality.

4. Pneophyllum limitatum (Foslie) Y. Chamberlain, comb. nov.

BASIONYM: *Melobesia lejolisii* forma *limitata* Foslie in *K. nor. Vidensk. Selsk. Skr.* **1905** (3): 102 (1905).

NOMENCLATURAL SYNONYMS: *Melobesia limitata* (Foslie) Rosenv. in *K. dansk. Vidensk. Selsk. Skr.* II, **7**: 245, Figs 163–167 (1917).

Fosliella limitata (Foslie) Ganesan in *Phykos* **2**: 41 (1963).

Heteroderma limitata (Foslie) Adey in *K. nor. Vidensk. Selsk. Skr.* **1970** (1): 16 (1970).

REFERENCES: *Melobesia limitata* (Foslie) Rosenv.; Suneson in *Acta Univ. lund.* II, **33**: 14 (1937), in *Acta Univ. lund.* II, **39**: 24 (1943); Kylin in *Acta Univ. lund.* II, **40**: 44 (1944); Hamel and Lemoine in *Archs Mus. natn. Hist. nat. Paris* VII, **1**: 105 (1953 ['1952']); Sundene in *Skr. nor. Vidensk. – Akad. mat.-nat. Kl.* **1953** (2): 192 (1954); Cabioch *In* Feldmann in *Trav. Stn biol. Roscoff* II, **15**: 17 (1964).

Fosliella limitata (Foslie) Ganesan; Parke & Dixon in *J. mar. biol. Ass. U.K.* **56**: 534 (1976); Chamberlain in *Br. phycol. J.* **12**: 69 (1977); Rueness, *Norsk algeflora*: 60 (1977); Garbary *In* D. E. G. Irvine and J. H. Price (Eds), *Modern approaches to the taxonomy of brown and red algae*: 205–222 Figs 13, 14 (1978); de Valéra, Pybus, Casley and Webster in *Proc. r. Ir. Acad.* **79** B: 265 (1979).

LECTOTYPE: TRH! Herb. Foslie, Coll. L. K. Rosenvinge, no. 3807, 22 August 1893, Lungfjorden, Lendrup Røn, on an air bladder of *Fucus vesiculosus*.

DIAGNOSIS: Mainly epiphytic with a well calcified thin thallus, trichocytes frequent, conceptacles conical and ostiole surrounded by long, segmented filaments united into a funnel: differing from *P. lejolisii* and *P. concollum* in having long ostiolar filaments, from *P. rosanoffii* in not having free, terete ostiolar filaments; and from *P. zonale* in not having a deep vegetative crust or free ostiolar filaments.

DESCRIPTION: Well-calcified, regular, dull mauvy-pink, mainly epiphytic crusts up to 10 mm diameter, *c.* 75 μm deep, perithallium absent except near conceptacles (up to 4 cells deep in crusts with flat bisporangial conceptacles), *crust cells* in surface view sharply rectangular, 6·5–20·5 μm long × 5·5–13·5 μm wide, *epithallial cells* 3–5·5 μm long × 5·5–10·5 μm wide, large branch cell or intrafilament *trichocytes* 14–26 μm long × 10·5–17 μm wide; conceptacles (except spermatangial and one bisporangial form) prominent, ostiole surrounded by funnel of fused segmented filaments, *carposporangial conceptacles* 117–169 μm internal diameter × 52–109 μm high, carposporangia densely crowded when mature, *spermatangial conceptacles* immersed beside carpogonial conceptacles, 33–59 μm wide × 21–30 μm deep, ostiole prolonged into a spout, *tetrasporangial conceptacles* 151–229 μm internal diameter × 68–117 μm high, tetrasporangia crowded, up to *c.* 30 per conceptacle, 31–60 μm long × 29–39 μm wide, OR conceptacles flat with simple ostiole, in thallus up to 6 cells deep, 65–96 μm internal diameter × 29–61 μm high, bisporangia peripheral, 23–39 μm long × 18–30 μm wide.

HISTORICAL: Foslie (1905*a*) described *P. limitatum* as a form of *P. lejolisii* (as *Melobesia*) with smoother, thicker crusts, and conceptacles which were more conical and widely spaced. The lectotype (Adey, 1970) is a Rosenvinge specimen (TRH) in which the crusts of *P. limitatum* are epiphytic on *Fucus vesiculosus*. According to Rosenvinge (1917, p. 245) Foslie came to regard *Melobesia lejolisii* f. *limitata* as mainly growing on algae as opposed to f. *typica* which mainly grew on marine phanerogams. Rosenvinge (1917) considered the features of forma *limitata* to be sufficiently distinct to warrant specific status as *Melobesia limitata*.

Pneophyllum limitatum has proved to be one of the commonest simple crustose coralline epiphytes in northern Europe and is common on Scandinavian, British, and northern French shores.

CRUST APPEARANCE: *P. limitatum* forms well calcified, rather regular, dull mauvy-pink crusts which are often crazed on the surface. The plants are predominantly epiphytic on algae, but are also found on marine phanerogams and occasionally on glass or china. When growing most vigorously, on large, intertidal algae in autumn, the crusts (Fig. 38) are regularly orbicular or confluent with other crusts, and may exceed 10 mm diameter; at other times the crusts are less regular and smaller. The conceptacles are usually well spaced out in the crust centre, with the crust border being vegetative only; sometimes two adjacent conceptacles fuse together. Even at low magnification the conceptacles are conspicuously conical, and the ostiolar funnel forms a characteristically pale ring (Fig. 39C) in the conceptacle centre.

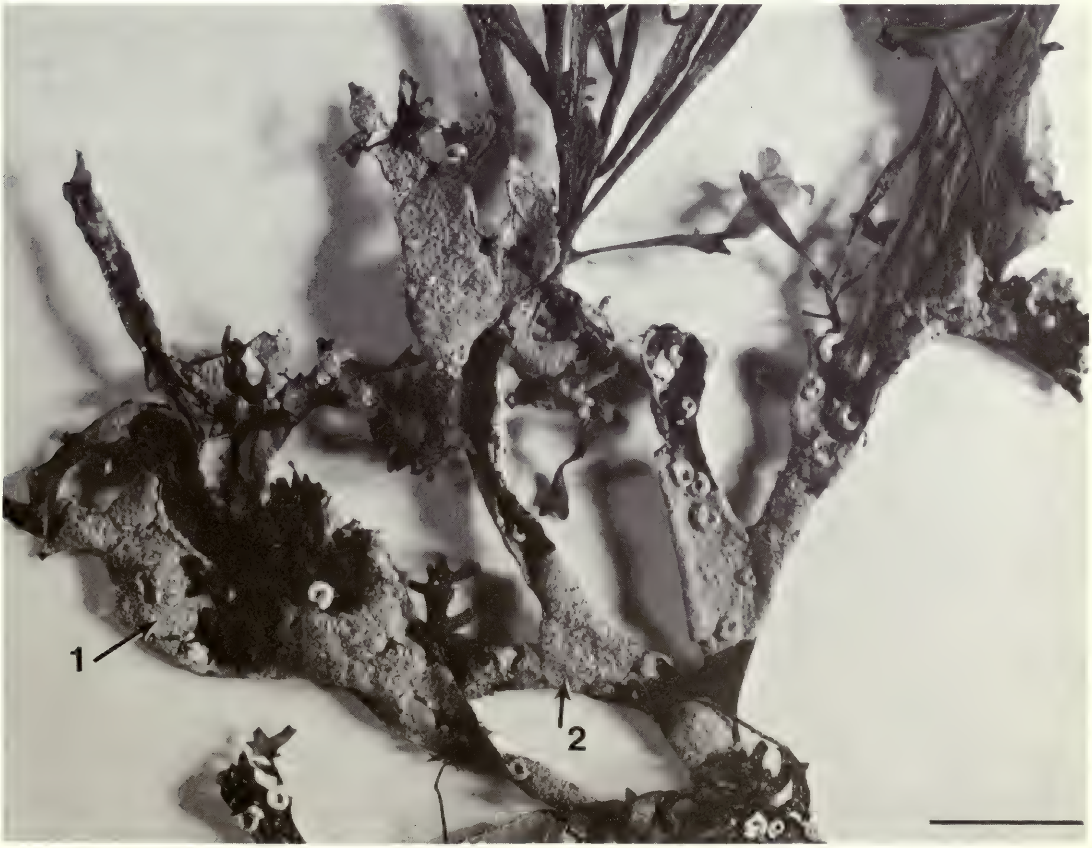


Fig. 38 *Pneophyllum limitatum* (1) and *Fosliella farinosa* (2) growing on *Chondrus crispus*. Scale = 10 mm.

Under the S.E.M. the crust cells (Fig. 39D) are broadly rectangular with short, wide, epithallial concavities and large branch cell and intrafilament trichocytes. In all types of conceptacle the roof is uniform (Figs 39A, B, C; 40A, B), and the inconspicuous spermatangial ostiole can be seen at the side of the carpogonial conceptacle (Figs 40A, F). The small type bisporangial conceptacles (Figs 39A, B) have a gently raised roof and a simple ostiole. The young conical conceptacle type has a plateau-like roof and simple ostiole (Fig. 40A); this later develops into a conical structure and the top of this may acquire a coating (presumably mucilaginous) as it senesces (Fig. 40E). The fused filaments of the funnel-like ostiole are very conspicuous, and the stages in their development and senescence are seen in Figures 40C–E. In the centre of the funnel is a further ring of filaments which forms a diaphragm-like structure (Fig. 40C).

VEGETATIVE ANATOMY: The crusts are composed of hypothallium and epithallium only, except near conceptacles, in all but the small type bisporangial conceptacles; these have 1–4 perithallial cells. The crust cells of all phases are sharply rectangular (Fig. 41A), with conspicuous epithallial cells. The trichocytes are usually noticeably larger than the surrounding crust cells, and are divided by a radial wall into a pigmented, hair-bearing part and a colourless part (see Chamberlain, 1977*a*); trichocytes usually lack epithallial cells. Suneson (1943) showed abnormal, very large, terminal trichocytes, and large, richly protoplasmic cells in some crusts of *P. limitatum*. I have not found these in this species, but have seen similar trichocytes in epilithic species such as *P. myriocarpum* (*q.v.*). Suneson (1943) considered the possibility that the rounded contents of the richly protoplasmic cells represented some form of vegetative reproductive body.

GAMETANGIAL PLANTS: Gametangial plants are monoecious; the spermatangial conceptacle (Figs 40A; 42C, F) is immersed in the thallus beside the carpogonial conceptacle; it is more or less oval in VS and about twice as wide as high, with the ostiole prolonged into a hyaline spout. Spermatangial initials usually produce elongated spermatangia from two sites; these round off into small, oval spermatangia when released. Spermatangium development is described and depicted by Suneson (1937).

The carpogonial conceptacle (Fig. 42C), is gently raised; its structure and development have been investigated and illustrated in detail by Suneson (1937). The conceptacle cavity develops by the elongation and final rupturing of the perithallial cells, while the upper surface of the perithallial cells gives rise to the roof filaments and the extensively developed ostiolar filaments. Suneson (1937, Figs 6E and 7) shows that the procarps in the centre of the fertile disc bear one or two carpogonia, while the peripheral procarps bear one or no carpogonia.

CARPOSPORANGIAL CONCEPTACLES: The typical carposporangial conceptacle (Fig. 42E) has one or, occasionally, two basal cell layers, a fairly thin roof with rather irregular cells, and a substantial fusion cell immediately above the basal cells. Suneson (1937) found that, while in most carposporangial conceptacles gonimoblast filaments were initiated only from the periphery of the fusion cell (as in all other known species of *Pneophyllum*), in some they were initiated over the entire fusion cell surface, which seemed to be unique for this genus. I previously concurred with this observation (Chamberlain, 1977*a*), but on further examination have found that while carposporangial filaments are very occasionally produced on the surface of the extreme periphery of the fusion cell in British material, they have not been found across the entire surface, and are mainly borne in the usual way from the actual periphery. Nevertheless, the fact that they are borne on the surface of the fusion cell at all is a distinguishing character. The size of the conceptacles varies considerably (Tab. 15), and in practice the conceptacles are usually larger when the plants are growing under optimum conditions. The discrepancy in conceptacle height dimension between the present values and those given by Suneson (1937, 1943) and Chamberlain (1977*a*) is due to the fact that the length of the ostiolar funnel is excluded from the present values. In general, there are one or two perithallial cells at the periphery of the conceptacle (Fig. 42E), and beyond these the crust quickly reverts to being composed of hypothallium and epithallium only. Another form has been found, however, which has a deep

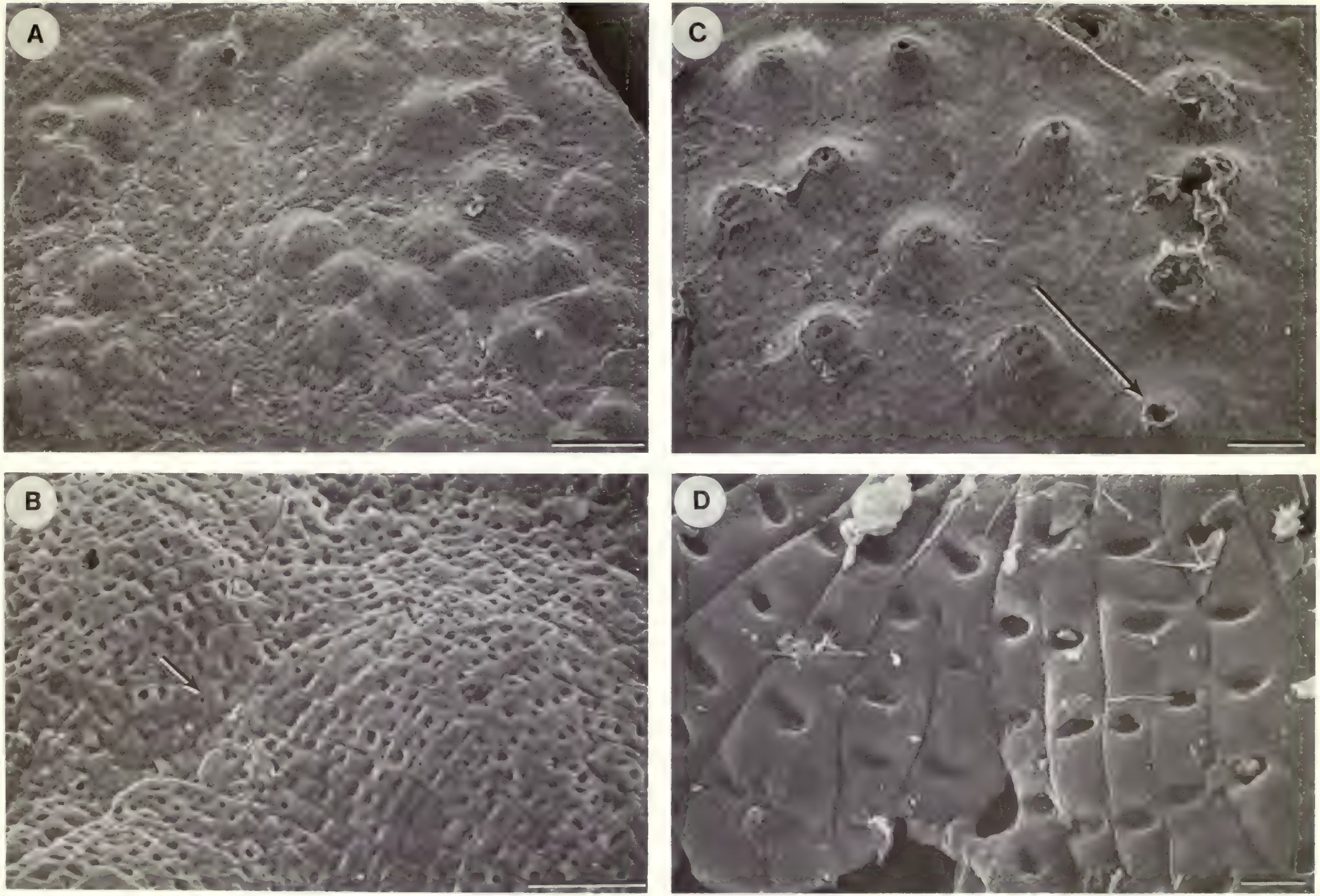


Fig. 39 Scanning electron micrographs to show crust features of *Pneophyllum limitatum*. A, Small type bisporangial crust showing the slightly raised conceptacles with small ostioles. Scale = 250 μm. B, Enlargement from A showing the simple ostiole and intercalary trichocytes (arrow). Scale = 50 μm. C, Tetrasporangial crust showing conical conceptacles, some with mature ostiole funnels (arrow). Scale = 250 μm. D, Crust periphery showing crust cells and epithallial concavities. Scale = 10 μm.

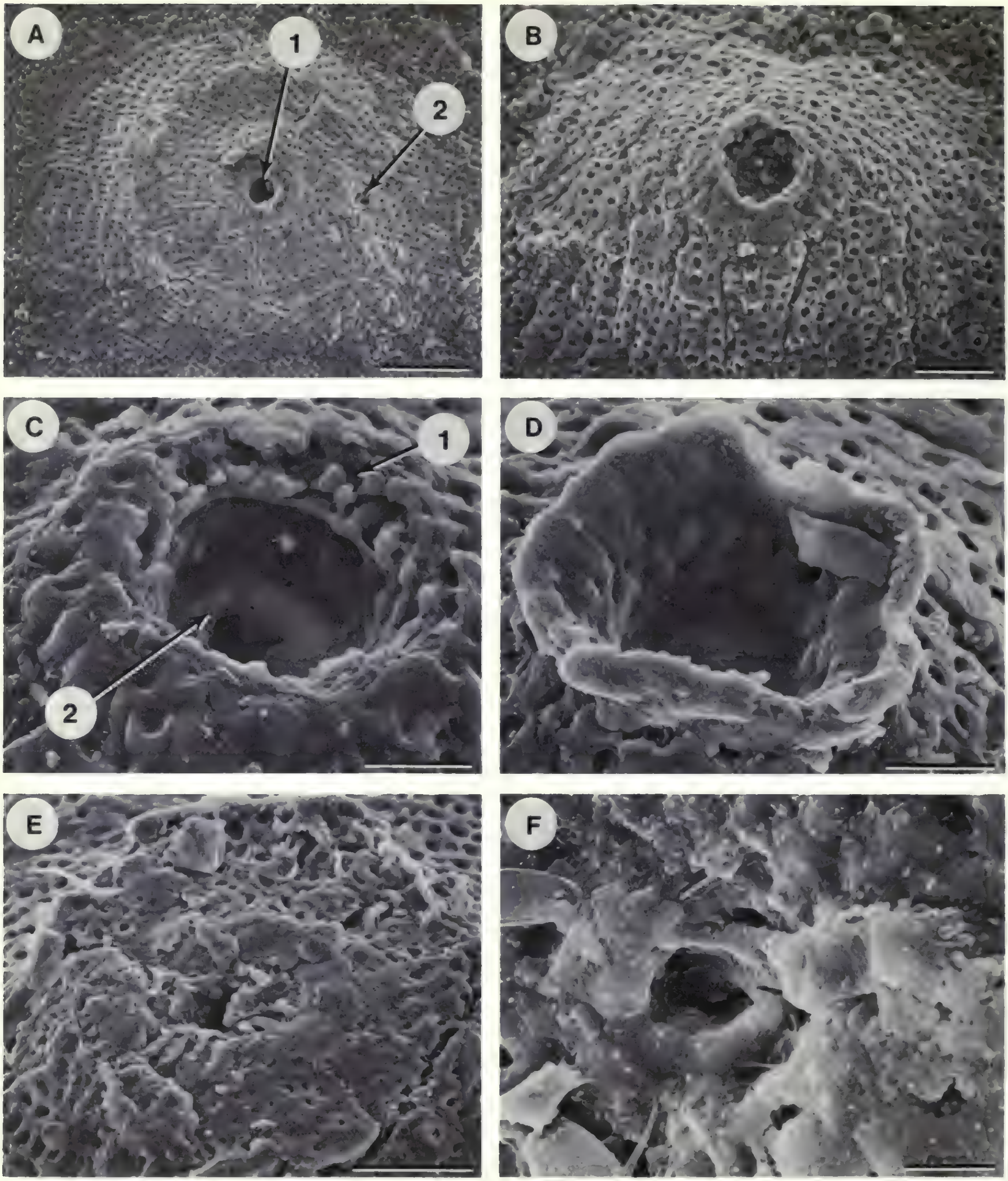


Fig. 40 Scanning electron micrographs to show conceptacle features of *Pneophyllum limitatum*. A, Carpogonial (1) and spermatangial (2) conceptacles at an early stage before the roof has become conical. Scale = 100 μm. B, Tetrasporangial conceptacle with developing ostiole funnel. Scale = 50 μm. C, Young carposporangial ostiole with outer ostiole filaments (1) developing and inner filament ring (2) visible. Scale = 25 μm. D, Mature funnel-like tetrasporangial ostiole. Scale = 25 μm. E, Senescent tetrasporangial conceptacle roof in which the ostiole has disintegrated. Scale = 50 μm. F, Spermatangial ostiole. Scale = 10 μm.

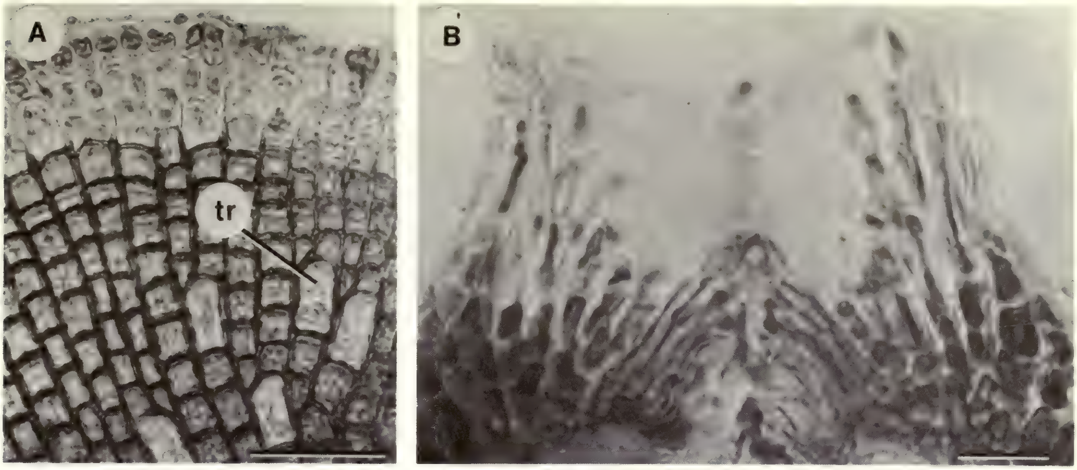


Fig. 41 Crust and ostiole features of *Pneophyllum limitatum*. A, Crust in surface view with trichocytes (tr). Scale = 50 μm. B, Vertical section of inner and outer rings of tetrasporangial ostiole filaments. Scale = 20 μm.

thallus and larger conceptacles; a similar form was illustrated by Rosenvinge (1917, Fig. 164). This form occurs in the two epilithic samples found at Bembridge and occasionally in epiphytic material.

The structure of the ostiolar filaments in VS is shown in Figure 41B, where it can be seen that they are segmented for much of their length. This differs from the unsegmented filaments of *P. zonale* and *P. rosanoffii*, with which this species may otherwise be confused. However, the fusion of the filaments to form a funnel is not obvious in decalcified sectioned material of *P. limitatum* although it can be seen clearly under the S.E.M. (Fig. 40D). The presence of an inner ring of filaments (Figs 40C; 41B) is also, as far as is known, unique to *P. limitatum*.

Large quantities of carposporangial filament cells and carposporangia are produced by *P. limitatum,* and the mature conceptacle is packed tightly with them as was also shown by Suneson (1937).

Tetrasporangial plants: The structure and development of tetrasporangial conceptacles (Figs 39C; 40B; 42D) follows the same pattern as in the carposporangial conceptacles. The tetrasporangia are borne peripherally on stalk cells (Fig. 42D); Suneson (1937) showed that young sporangia develop among sterile cells within a balloon-like sac, and are deeply divided into four from an early stage. As with the carposporangia, large numbers of tetrasporangia are produced in each conceptacle and these are piled high in the mature conceptacle. Sometimes the ostiolar filaments have been observed to develop deep within the conceptacle, and some sections of this type of structure resemble procarps (Chamberlain, 1982).

Bisporangial plants: As has already been mentioned, two types of bisporangial conceptacle occur in *P. limitatum*. One form (Fig. 42B) is similar to the tetrasporangial conceptacles, except that it produces uninucleate bispores (which are presumed to be diploid) instead of tetraspores. This form has been found only occasionally in the British Isles and has not been recorded previously.

The other form (Figs 39A, B; 42A) has a quite different aspect, although the vegetative crust border has crust cells similar to *P. limitatum* cells. The thallus of this form has perithallial filaments up to four cells deep and the perithallial cells are more or less isodiametric in VS. The conceptacles are immersed in the thallus and have a simple ostiole. The bisporangia are borne peripherally and are more rounded than in the other bisporangial conceptacle type, while relatively few bisporangia (probably not exceeding 10) occur in each conceptacle. This type of conceptacle was first recorded and figured by Suneson (1937); it is quite easy to identify under optimum conditions when it occurs among crusts with conical conceptacles, but crusts found in

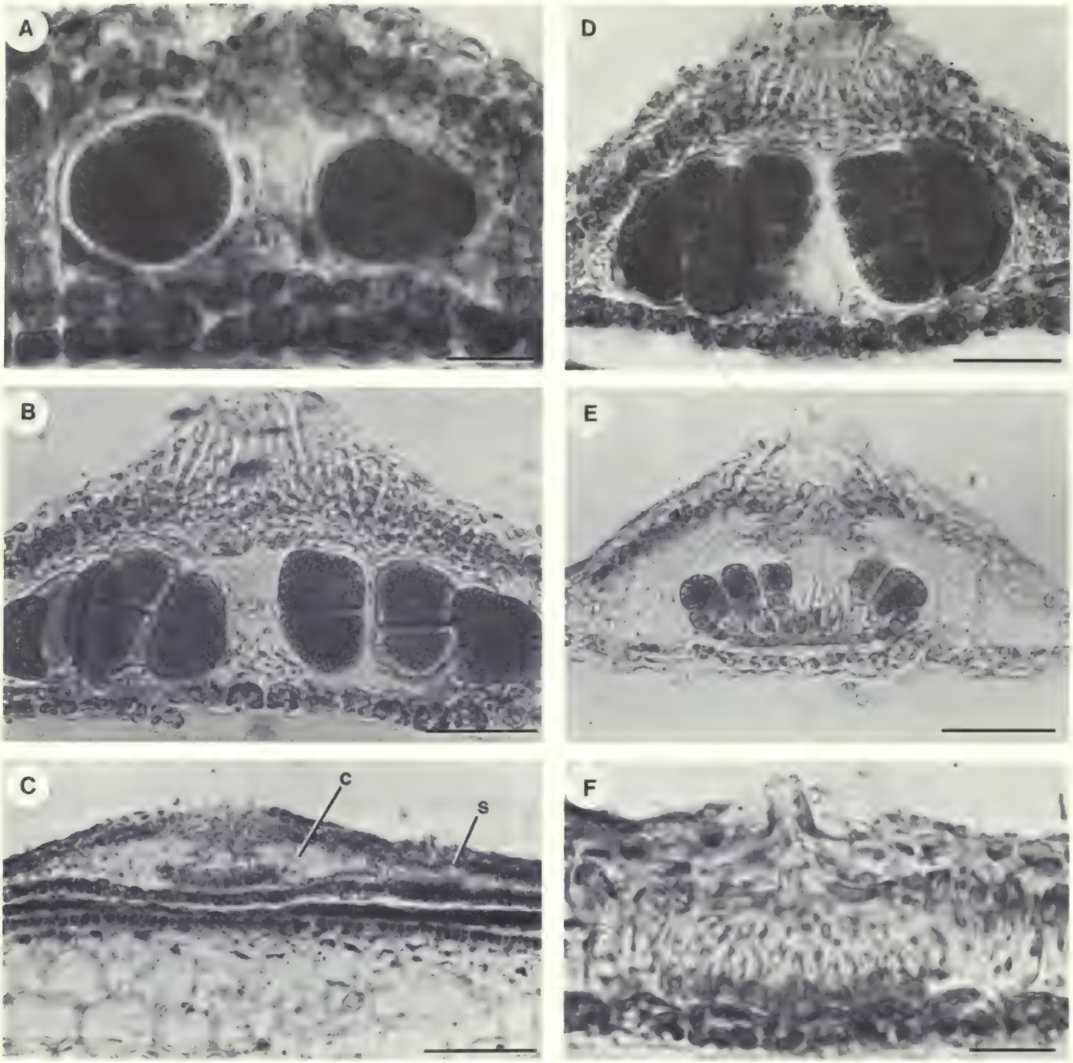


Fig. 42 Vertical sections of conceptacles of *Pneophyllum limitatum*. A, Flat type of bisporangial conceptacle. Scale = 20 μm. B, Domed type of bisporangial conceptacle. Scale = 50 μm. C, Gametangial crust showing carpogonial (c) and spermatangial (s) conceptacles. Scale = 100 μm. D, Tetrasporangial conceptacle. Scale = 50 μm. E, Carposporangial conceptacle. Scale = 50 μm. F, Spermatangial conceptacle. Scale = 20 μm.

isolation are virtually impossible to distinguish from, for example, bisporangial crusts of *P. microsporum*. *P. limitatum* is the only species in which two bisporangial conceptacle types have been identified.

PHENOLOGY: *P. limitatum* occurs throughout the year on the shores of the British Isles (see Chamberlain, 1977*a*), but it is most abundant and vigorous during autumn and early winter (September to November). At this time it has been observed at Bembridge on a wide range of intertidal algae, but particularly on the fronds of *Laminaria digitata, L. saccharina, Fucus serratus, Chondrus crispus,* and *Palmaria palmata*; it usually grows together with *Fosliella farinosa* (Fig. 38) at this season, but *F. farinosa* tends to become more abundant and *Pneophyllum limitatum* less so as winter deepens. However, the degree of abundance depends on the weather and in 1975, 1976, and 1980 this bloom was much more in evidence than in the years between or since.

A collection of *Pneophyllum limitatum* on *Palmaria* is present in Le Jolis's herbarium (CHE). It was collected in the Cherbourg area (Le Jolis no. 240, 30 November 1853). Le Jolis originally identified the crusts as *Melobesia pustulata,* while Rosanoff (1866) reidentified them as *M. farinosa* and *M. pustulata*. It seems probable, therefore, that a bloom of *Pneophyllum limitatum*, similar to that seen in England, occurs in autumn in northern France, and this was corroborated by a collection made in October 1981 at Hercquemoulin on the northwestern side of the Cotentin peninsula, in which *P. limitatum* was abundant on several shore algae, particularly *Sargassum muticum.*

FORM RANGE: As has been mentioned, the crusts of *P. limitatum* tend to be larger and more regular in autumn than at other seasons. Trichocytes are more abundant at this time, and absent from about November until June. Crust cells tend to be smaller and relatively longer under less favourable conditions; the dimensions given in Table 14 were made on material collected in September, while in material collected during November trichocytes were absent, crust cells measured (7) 10 (14) μm long × (4) 7 (9) μm wide, and epithallial cells were *c.* 3 μm long × 2–5 μm wide.

As noted previously (Chamberlain, 1977*a*), *P. limitatum* crusts growing on *Zostera* tend to have more abundant trichocytes than those growing on algal hosts.

As has been discussed, the conical type of bisporangial conceptacle occurs very rarely in Britain, while the flat roofed type is common here and in Sweden (Suneson, 1937); it has also been observed in material from Normandy. In a single collection made in Brittany conical bisporangial conceptacles were frequent, but no flat-roofed ones were seen, nor have flat-roofed conceptacles been observed in Irish material.

DISTRIBUTION:
British Isles: Recorded throughout the British Isles with the exception of the east coasts of England and Scotland. *P. limitatum* is the commonest epiphytic *Pneophyllum* on algae in south and south-west England, as it is in Scandinavia, but it seems possible that its place is taken to some extent by *P. concollum* in Ireland, where *P. limitatum* is generally less common, although it was abundant in one collection of algae from Co. Clare made in November 1981.
World: Norway, Sweden, Denmark, northern France.

Table 14 Dimensions of vegetative structures (in μm unless stated).

Pneophyllum limitatum	British Isles	Rosenvinge (1917)	Suneson (1937, 1943)
crust diameter	up to 10 mm	up to 5 mm	up to 5(10) mm
crust depth	*c.* 75		
crust cell length	(6·5) 10·5 (20·5)	(7) 8–10	(11) 13–16
surface width	(5·5) 10 (13·5)	(5)–12	(5) 6–10
crust cell height	*c.* 15–20		
epithallial cell length	(3) 4 (5·5)		
surface view width	(5·5) 7·5 (10·5)		
epithallial cell height	*c.* 5–8		
hypothallial cell width			
VS height			
perithallial width			
cell height			
VS number			
trichocyte type	branch cell and intercalary		
trichocyte length	(14) 21 (26)		up to 22
surface view width	(10·5) 12 (17)		

Table 15 Dimensions of reproductive structures (μm unless stated).

Pneophyllum limitatum	British Isles	Rosenvinge (1917)	Suneson (1937, 1943*a*)
CARPOSPORANGIAL CONCEPTACLE			
external diameter		210–325	90–210
surface diameter	(143) 165 (177)		
VS internal diameter	(117) 141 (169)		90–115
VS height	(52) 78 (109)		100–180
VS roof height	(8) 17 (26)		
roof type	uniform		
no. basal cell rows	1 (rarely up to 4)		
ostiole	funnel shaped		
no. gonimoblast filaments			
diameter carpospore			
SPERMATANGIAL CONCEPTACLE			
VS/surface width	(33) 44 (59)	56	70
VS height	(21) 26 (30)		56
length spermatium			
width spermatium			
TETRASPORANGIAL CONCEPTACLE			
external diameter		(170) 230–325	140–270
surface diameter	(138) 162 (182)		
VS internal diameter	(151) 177 (229)		150–240
VS height	(68) 92 (117)		
VS roof height	(10) 17 (26)		
roof type	uniform		
no. basal cell rows	1 (rarely up to 4)		
ostiole	funnel shaped		
no. tetrasporangia	up to *c.* 30+		
length tetrasporangium	(30) 53 (60)	46–77	
width tetrasporangium	(29) 32·5 (39)	21–46 (61)	
BISPORANGIAL CONCEPTACLE			
external diameter			75–125
surface diameter			
VS internal diameter	(65) 82 (96) [156 210 234]		
VS height	(29) 45 (61) [65 80 91]	60–70	60–110
VS roof height	(10) 13 (18) [13 17 21]		
roof type	uniform [uniform]		
no. basal cell rows	1–3 [1]		
ostiole	simple [funnel-shaped]	simple	simple
no. bisporangia	up to *c.* 10 [*c.* 30+]		
length bisporangium	(23) 30 (39) [39 48 52]		33
width bisporangium	(18) 22·5 (30) [23 30 36]		23

[] large type bisporangial conceptacle

HABITAT: Epiphytic on a wide range of intertidal algae, but particularly on *Palmaria palmata, Fucus serratus, Laminaria saccharina*, and *L. digitata,* where it usually grows together with *Fosliella farinosa*. It also occurs quite commonly on *Zostera*, usually together with *Pneophyllum lejolisii*, and has very occasionally been found occurring epilithically.

In Denmark (Rosenvinge, 1917) *P. limitatum* was found most commonly on *Fucus vesiculosus* (an alga which rarely supports crustose coralline epiphytes in the British Isles), but also grew on other algae and frequently occurred together with *Dermatolithon pustulatum* (as *Lithophyllum macrocarpum*).

LIFE HISTORY: No experimental evidence is yet available regarding the life history of *P. limitatum*. It would be particularly interesting to obtain information on the life history of this species in view of the two types of bisporangial crust which occur.

5a. Pneophyllum confervicolum (Kütz.) Y. Chamberlain comb. nov.
Forma confervicolum

BASIONYM: *Phyllactidium confervicolum* [‘*confervicola*’] Kütz., *Phycologia generalis*: 295 (1843).

NOMENCLATURAL SYNONYMS: *Hapalidium phyllactidium* (Kütz.) Kütz., *Species algarum*: 695 (1849).
Hapalidium confervicolum (Kütz.) Areschoug *In* J. G. Agardh (Ed.), *Species, genera et ordines algarum*: 509 (1852).
Hapalidium confervoides (Kütz.) P. Crouan & H. Crouan pro parte (?), *Florule du Finistère*: 149 (1867).
Melobesia confervicola (Kütz.) Foslie in *K. nor. Vidensk. Selsk. Skr.* **1900** (5): 21 (1900).

REFERENCES: (?) *Lithocystis allmanni* Allman *In* Harvey, *Phycologia Britannica*: pl. CLXVI (1948).
Hapalidium phyllactidium (Kütz.) Kütz.; Kützing, *Tabulae phycologicae*: 33, tab. 92 c–d (1869); Crouan P.-L. and H.-M. in *Annls Sci. nat. Bot.* IV, **12**: 286, pl. 21, figs 14–20 pro parte? (1859) [see Fig. 44].
(?) *Melobesia inaequilaterata* Solms-Laub. in *Fauna Flora Golf Neapel* **4**: 12 (1881).
(?) *Heteroderma inaequilaterata* (Solms-Laub.) Foslie in *K. nor. Vidensk. Selsk. Skr.* **1909** (2): 56 (1909).
Melobesia minutula f. *typica* Foslie in *K. nor. Vidensk. Selsk. Skr.* **1905** (3): 107 (1905); Rosenvinge in *K. danske Vidensk. Selsk. Skr.* II, **7**: 252 (1917); Knight & Parke, *Manx algae*: 102, 108 (1931); Suneson in *Acta Univ. lund.* II, **39**: 27 (1943); Hamel & Lemoine in *Archs Mus. natn. Hist. nat. Paris* VII, **1**: 107 (1953 [‘1952’]); Feldmann in *Trav. Stn biol. Roscoff* Supplement **6**: 78 (1954); Zinova, *Check-list of green, brown and red algae of the southern seas of the U.S.S.R.*: 232 (1967).
Melobesia fosliei Rosenvinge in *K. danske Vidensk. Selsk. Skr.* II, **7**: 249 (1917).
Melobesia fosliei sensu Kylin in *Acta Univ. lund.* II, **40**: 45 (1944).
Heteroderma minutula (Foslie) Dawson in *Pacif. Sci.* **10**: 47 (1956); Adey in *K. nor. Vidensk. Selsk. Skr.* **1970** (1): 16 (1970).
Fosliella minutula (Foslie) Ganesan in *Phykos* **2**: 38 (1963); Parke & Dixon in *J. mar. biol. Ass. U.K.* **56**: 534 (1976); Rueness, *Norsk algeflora*: 60 (1977).

HOLOTYPE: L! 941.156.120. Herb. Kützing, near Trieste, on ‘*Conferva vasta*’ (Figs 43A, B; 45A).

DIAGNOSIS: Epiphytic species with small, square crust cells, very short, wide epithallial cells and abruptly hemispherical conceptacles: differing from *Fosliella farinosa* in having intercalary (not terminal) trichocytes and lacking trichocytes round conceptacle base, from *Pneophyllum lejolisii* in having domed conceptacles and isodiametric crust cells.

DESCRIPTION: Crusts pale to mauvy-pink, not exceeding 2 mm diameter, perithallium absent except near conceptacle in some forms, *crust cells* in surface view typically isodiametric, 5·5–13·5 μm long × 4–14·5 μm wide, *epithallial cells* short and wide, 1·5–4 μm long × 2·5–8 μm wide, intrafilament or branch cell trichocytes similar to crust cells in size or sometimes longer; conceptacles abruptly hemispherical, all except spermatangial conceptacles with simple ostiole, or with a small beak, or occasionally with ostiole filaments, *carposporangial conceptacles* 47–104 μm internal diameter × 39–68 μm high, *spermatangial conceptacles* c. 30 μm wide × 23 μm high, ostiole prolonged into a spout, *tetrasporangial conceptacles* 52–91 μm internal diameter × 30–74 μm high, up to 10 tetrasporangia per conceptacle, 26–46 μm long × 15·5–27·5 μm wide; *bisporangial conceptacles* 68–107 μm internal diameter × 52–65 μm high, bisporangia 26–39 μm long × 14·5–21 μm wide.

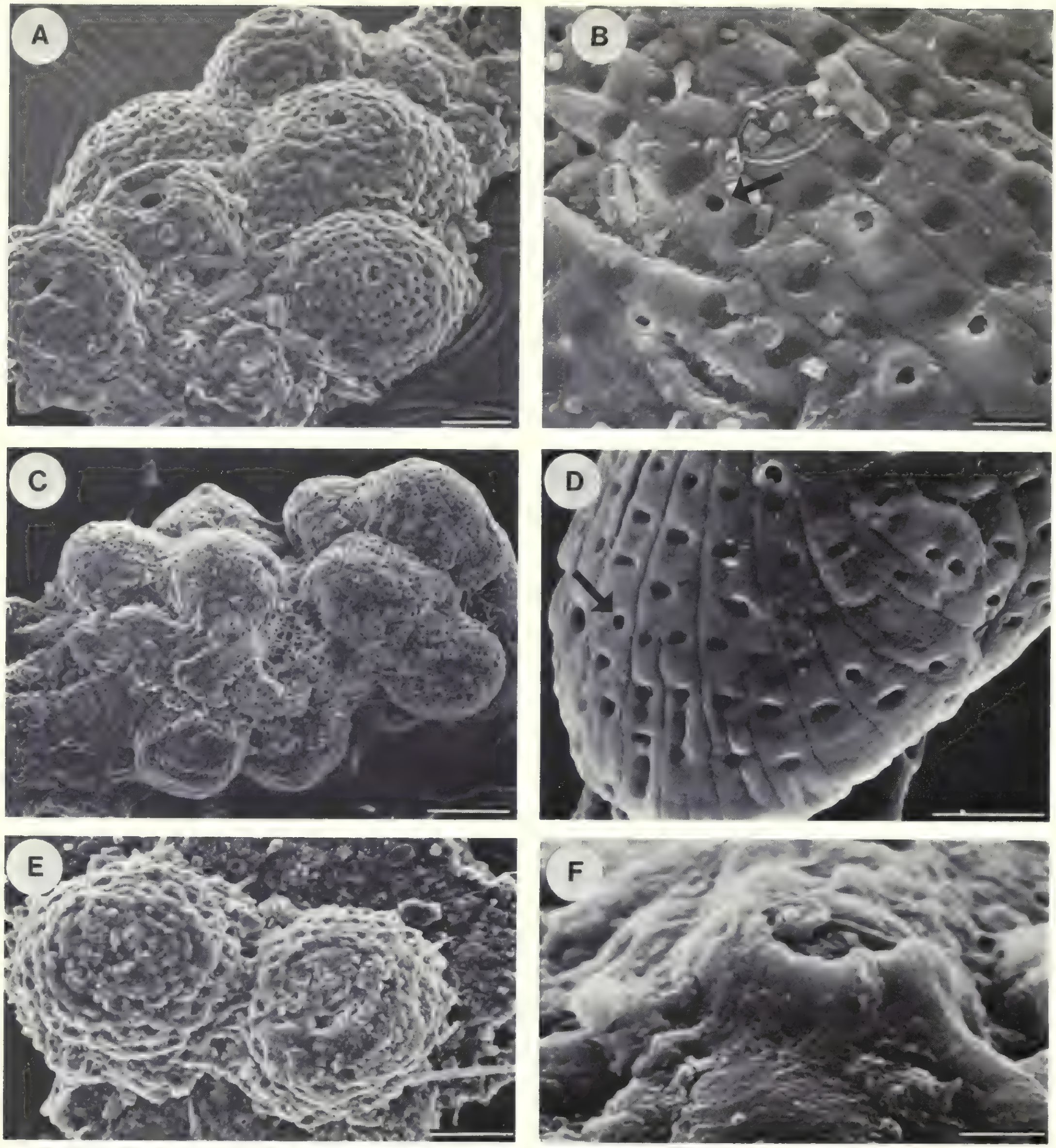


Fig. 43 Scanning electron micrographs of *Pneophyllum confervicolum* f. *confervicolum*. A, Type specimen of *Phyllactidium confervicolum* Kütz. (L.). Scale = 50 μm. B, Crust cells from A; trichocytes (arrow) present. Scale = 10 μm. C, Crusts from Ardkeen growing on *Cladophora rupestris*. Scale = 50 μm. D, Crust cells from C; trichocytes (arrow) present. Scale = 25 μm. E, Crusts from Bembridge growing on *Furcellaria lumbricalis*. Scale = 50 μm. F, Beaked ostiole. Scale = 5 μm.

Historical: *P. confervicolum* was originally described by Kützing (1843, p. 295) as *Phyllactidium confervicola,* a green calcareous alga epiphytic on *Chaetomorpha vasta* from Trieste. Later, Kützing (1849) realised that the five species he had included in *Phyllactidium* (Kützing, 1843) belonged to several different algal groups and he moved *confervicolum* to *Hapalidium*, a genus of coralline algae he had described earlier (Kützing, 1843) as having a monostromatic thallus and no cortical cells. Rosanoff (1866), however, later showed cortical cells to be present.

The type specimen (Figs 43A, B; 45A) of *Pneophyllum confervicolum* f. *confervicolum* (L – no. 941.156.120) agrees with the present concept.

The Crouan brothers (1859) included *Hapalidium phyllactidium* Kütz. in their notes on the genus *Hapalidium*. They recorded it as being epiphytic on various algae or *Zostera* and epilithic on glass and china. Material seen in Herb. Crouan (CO) was all on glass or china; it comprised a mixture of epilithic species of *Pneophyllum* but did not include *P. confervicolum* as now circumscribed. The Crouans' drawings, however, (Fig. 44C) may illustrate epiphytic material, since the crust shown in their Figure 16 appears to arise from a cellular substrate; the crust has square cells and prominent tetrasporangial conceptacles and may represent the present species. The Crouans (1867) included *P. confervicolum* in the *Florule du Finistère*; they had changed the specific epithet from *Hapalidium phyllactidium* to *H. confervoides* (Kütz.) J. Ag., although Areschoug (1852) in J. Agardh had spelled it *confervicolum*. Foslie (1900*a*) discussed the publications of the Crouans (1859, 1867) concerning *Hapalidium confervoides* and described the Crouans' epilithic material of it which he had obtained from PC: he concluded that the material was identical with *Melobesia zonalis* (P. Crouan & H. Crouan) Foslie and different from *Hapalidium phyllactidium* Kütz.

It seems possible that *Lithocystis allmanni* Allman in Harvey (1848) is conspecific with *Pneophyllum confervicolum* judging by the small, square cells in Harvey's illustration. Unfortunately the type specimen cannot be found at present so it is not possible to be sure.

Foslie (1905*a*) discussed *Epilithon van heurckii* which Heydrich (in Chalon, 1905) described on the basis of Chalon's material from Jersey. Foslie had received material from Chalon and he considered it to be conspecific with *Melobesia minutula*. However, the illustration (Heydrich in Chalon, 1905, p. 207) shows a bisporangial crust with a multiporate conceptacle roof. It cannot, therefore, belong to the genus *Pneophyllum,* and is now regarded as a species of the lithothamnioid genus *Melobesia*.

Danish material of *Melobesia minutula* was described by Rosenvinge (1917) who showed, contrary to the opinions of Kützing and Foslie, that the species usually bore cortical cells (epithallium). Rosenvinge (1917) described another species, *M. fosliei*, which differed from *M. minutula* only in possessing (intercalary) trichocytes. Suneson (1943) subsumed *M. fosliei* in *M. minutula*.

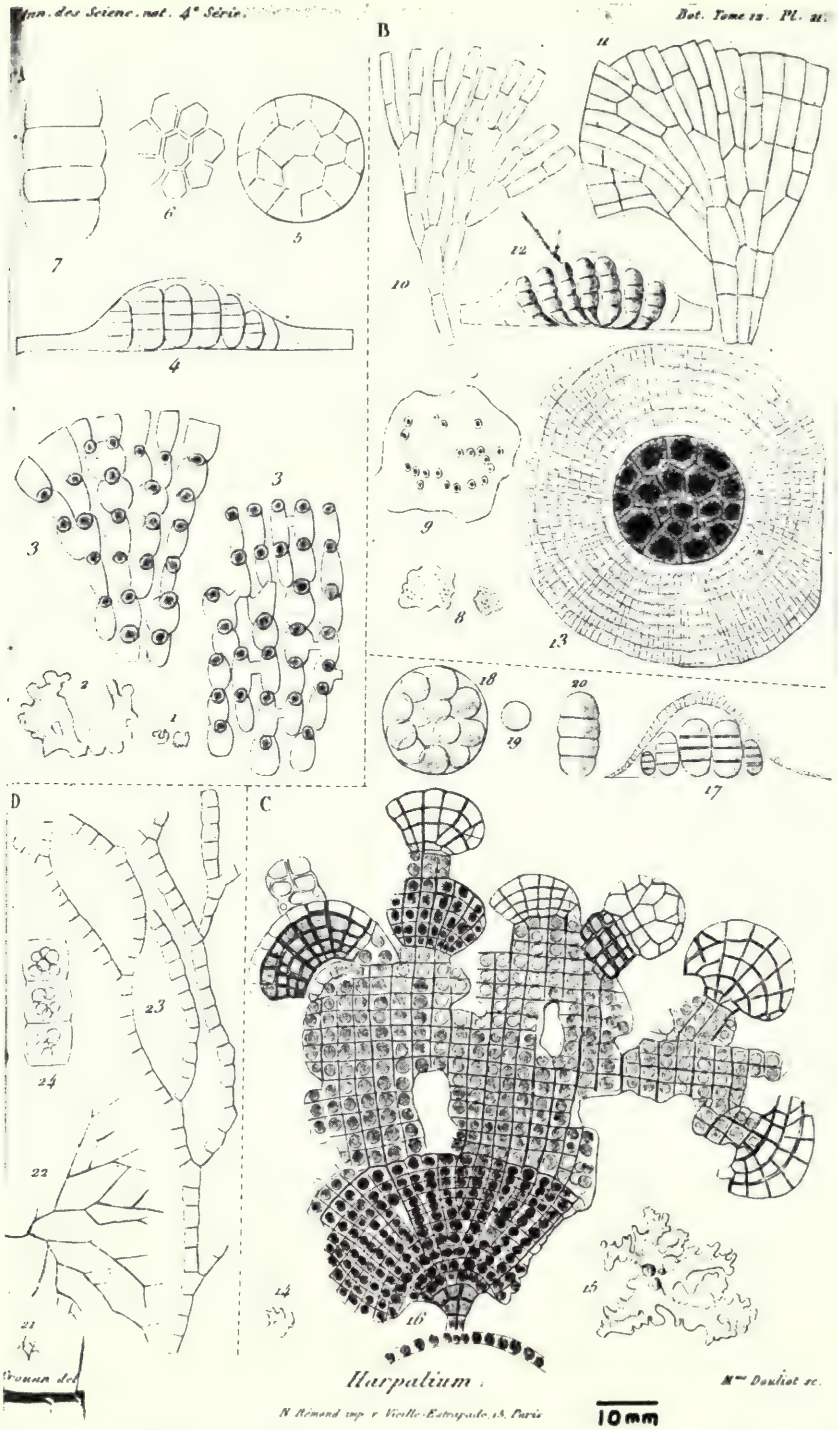
Kylin (1944) used the epithet *M. fosliei* as a synonym of *M. minutula* f. *typica* and restricted *M. minutula* Foslie to forma *lacunosa*.

Ganesan (1963) described material from India which agrees with the present concept and he transferred the species to the genus *Fosliella*.

CRUST APPEARANCE: The crusts of *P. confervicolum* vary considerably in appearance depending on their host. On *Zostera* and algae with flat thalli the small crusts (up to about 2 mm diameter) are pale and delicate; they may be regularly discoid, lobed, or show stages between this and the creeping filaments of f. *minutulum*. The conceptacles are hemispherical and scattered. On *Cladophora* and other algae such as *Plocamium* with narrow thalli, the conceptacles are so densely crowded (Fig. 43C) as to give the host a knobbly appearance. It is difficult to see the extent of the crusts in these circumstances, but many individual crusts probably bear only one or a few conceptacles; these crusts are often bright pink.

Under the S.E.M., the shape of the broad crust cells and very short, wide epithallial cells are shown in Figure 43D, while intercalary trichocytes are shown in Kützing's type material (Fig. 43B) and English material (Fig. 43D). The domoid conceptacles may have a stepped appearance (Figs 43A, E), or a somewhat irregular but smoother surface (Fig. 43C). In this, as in all other features, this species shows considerable variation.

VEGETATIVE ANATOMY: The vegetative crust is composed of epithallium and hypothallium only, and the crust cells (Figs 45D; 46A, B) are characteristically small and almost isodiametric with extremely short, broad epithallial cells. Sometimes, however, the cells are longer and narrower as shown by Suneson (1943). Intrafilament and branch cell trichocytes occur. Usually these are of similar length to the crust cells but bulge somewhat. Sometimes they are longer than the crust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Crouan del.
Harpalium.
Mme Douliot sc.
N. Rémond imp. r. Vieille-Estrapade, 15, Paris
10mm

Fig. 44 Plate from *Notice sur le genre Hapalidium* by Crouan & Crouan (1859). ('*Harpalium*' at the foot of the plate is presumably a printer's error). A, *Hapalidium zonale*. B, *Hapalidium coccineum*. C, *Hapalidium phyllactidium*. D, *Hapalidium callithamnioides*.

cells with a large pigmented part and a narrow unpigmented strip down one side (Figs 45D; 46B).

Gametangial plants: The crusts are monoecious. The spermatangial conceptacles are borne in the thallus at the edge of the carpogonial conceptacles and have the ostiole prolonged into a spout (Suneson 1943: 30 as *Melobesia minutula*). The raised carpogonial conceptacle (Fig. 45E) contains procarps bearing up to two carpogonia.

Carposporangial conceptacles: Carposporangial conceptacles are more or less hemispherical (e.g. Figs 45F–H). They may rise very abruptly from the thallus as in material from Lough Ine growing on *Gelidium*, and plants growing on *Corallina,* while on *Plocamium,* for example, they rise more gradually (Figs 45H; 46F). On *Cladophora* (Fig. 45G) the conceptacles are so crowded that sections often appear to show a thallus with perithallial development which is really the walls of adjacent conceptacles. The ostiole structure is very variable as was found also by Rosenvinge (1917, as *M. fosliei*) and Suneson (1943). Sometimes the ostiole is very simple with no development of either upper or lower filaments. Sometimes the lower ostiole filaments become quite well developed (Figs 45H; 46F), while the upper filaments may be prolonged into a small collar (Fig. 45F) or a spout (Fig. 45G), (see also Rosenvinge, 1917, fig. 169; Suneson, 1943: 30). On one occasion a conceptacle with well developed, upper ostiole filaments (Fig. 46G) was found among others with simple or slightly beaked ostioles. The fusion cell (Fig. 46F), is rather flat and bears carposporangial filaments peripherally.

Tetrasporangial conceptacles: Tetrasporangial conceptacles show a similar range of structure and size to carposporangial conceptacles. Abruptly hemispherical conceptacles are seen in Lough Ine material (Fig. 46D) and on *Furcellaria* from Bembridge (Fig. 45B), and more gently raised ones from Fanore (Fig. 45C). Beaked ostioles occur as illustrated by Suneson (1943: 29). Young tetrasporangia are thin, deeply divided into four, and enclosed in a hyaline, balloon-like sac (Fig. 46D). The farctate mature tetrasporangia are large in relation to the size of the conceptacle and usually entirely fill the cavity.

Bisporangial conceptacles: Bisporangial conceptacles show the same variety of structure as carposporangial and tetrasporangial conceptacles; an abruptly hemispherical form from Lough Ine is shown in Figure 46C, while a more gently rounded one with more developed ostiolar filaments is seen in Figure 46E of material from Fanore, Co. Clare, growing on *Plocamium*.

Phenology: *P. confervicolum* has been found throughout the year in the British Isles but is most common from May to November.

Form range: It is apparent from the species description that *P. confervicolum* shows a wide range of variation in the structure of the conceptacles and that sometimes the crust cells are not the very characteristic, isodiametric shape with very short, wide epithallial cells. In addition one Irish population growing on *Zostera* has the characteristic isodiametric crust cells (Fig. 46B), but they measure on average 10·5 μm long × 11 μm wide which is considerably larger than usual (Tab. 16). *P. confervicolum* is usually recognisable by its external appearance: the thin, delicate crust and minute bubble-like conceptacles are tiny compared with most other crustose, epiphytic corallines. Figure 45F shows *P. confervicolum* growing on a conceptacle of *Melobesia membranacea* in comparison with which it looks very small, although *M. membranacea* itself is not large. *Pneophyllum confervicolum* is most easily confused with the gametangial and tetrasporangial plants of *Fosliella farinosa* which may be very similar, although when trichocytes are present the two species are readily separated. In addition both species produce filamentous forms, but the difference in cell shape is usually apparent and can be seen in Figure 20B, where both are growing on *Gelidium* at Lough Ine. It remains possible, however, that distinct varieties, or even species, are present among the forms described here and further investigation of this taxon is needed.

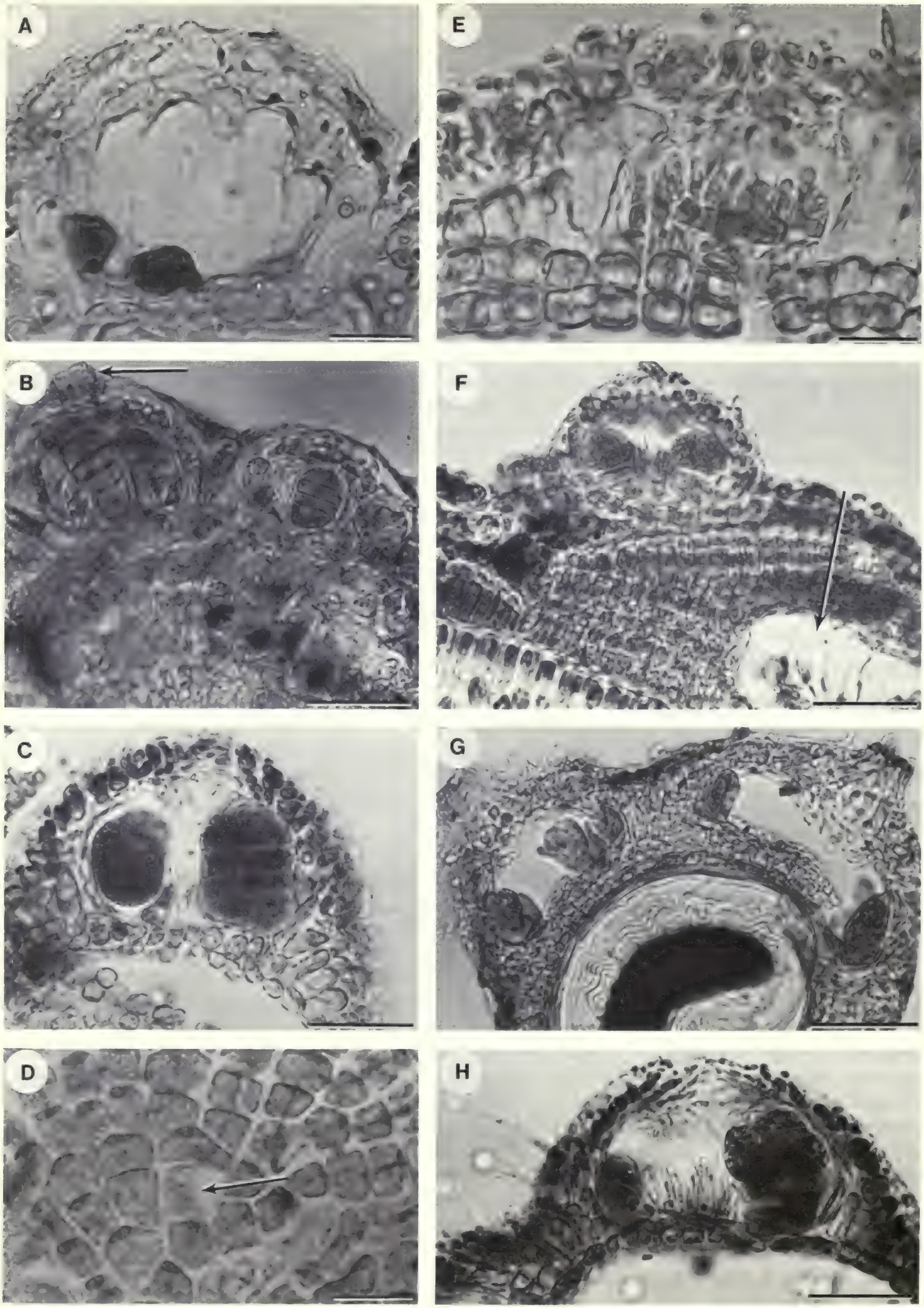
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Fig. 45 Thallus features and conceptacle variation in *Pneophyllum confervicolum* f. *confervicolum*. A, Vertical section of the type specimen *Phyllactidium confervicolum* Kütz. (L). Scale = 20 μm. B, Vertical section of tetrasporangial conceptacles growing on *Furcellaria lumbricalis* at Bembridge; ostiole plug arrowed. Scale = 50 μm. C, Vertical section of tetrasporangial conceptacle growing on *Plocamium coccineum* at Fanore, Co. Clare. Scale = 50 μm. D, Thallus cells growing on *Zostera marina* at Black Head, Co. Clare, with trichocyte (arrow). Scale = 20 μm. E, Vertical section of young carposporangial conceptacle growing on *Plocamium coccineum* at Fanore, Co. Clare. Scale = 20 μm. F, Vertical section of carposporangial conceptacle growing on conceptacle of *Melobesia membranacea* (arrow) at Bembridge. Scale = 50 μm. G, Vertical section of carposporangial conceptacles with spout growing on *Cladophora rupestris* at Ardkeen. Scale = 50 μm. H, Vertical section of carposporangial conceptacle growing on *Plocamium coccineum* at Fanore, Co. Clare. Scale = 50 μm.

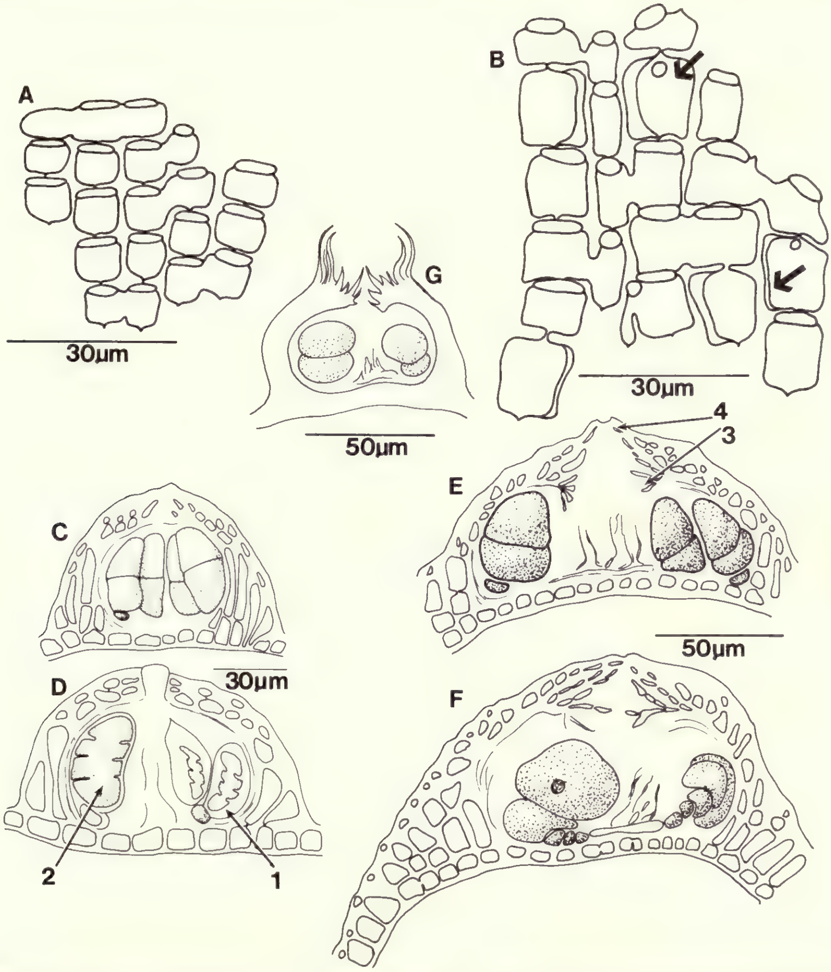


Fig. 46 *Pneophyllum confervicolum*. A, Decalcified crust in surface view to show typically small, isodiametric crust cells with very short epithallial cells. B, Decalcified crust from Irish material with larger crust cells, showing intrafilament trichocytes (arrows) with very narrow colourless parts. C, Vertical section of bisporangial conceptacle of abruptly hemispherical type (Lough Ine, Ireland). D, Vertical section of tetrasporangial conceptacle of abruptly hemispherical type, with young tetrasporangia in balloon-like sacs (1) and nearly mature tetrasporangium (2) (Lough Ine, Ireland). E, Vertical section of bisporangial conceptacle of rounded type with downward ostiole filaments (3) and small beak (4) (Fanore, Ireland). F, Vertical section of carposporangial conceptacle of similar type to E (Fanore, Ireland). G, Vertical section of carposporangial conceptacle with elaborate ostiole filaments found among normal hemispherical conceptacles (Bembridge).

DISTRIBUTION

British Isles: Hampshire, Dorset, Devon, Cornwall, Isle of Man, Anglesey, Mull, South Uist, Shetland, Channel Islands, Co. Antrim, Co. Down, Co. Wexford, Co. Cork, Co. Clare, Co. Galway.

World: Sweden, Norway, Denmark, France (northern and Mediterranean), Madeira, Italy, southern U.S.S.R., India, Pacific Mexico, central Pacific.

As Dawson (1960) has remarked, it is probable that this species occurs widely in tropical and temperate regions of the world, but its small size has caused it to be overlooked in many collections.

HABITAT: *P. confervicolum* has been found on a wide range of algal hosts and on *Zostera marina*; it also grows on bryozoans and hydroids. It is most abundant on warm, sheltered shores, like those of Lough Ine and Kimmeridge (Chamberlain, 1982).

5b. Pneophyllum confervicolum forma minutulum (Foslie) Y. Chamberlain, comb. nov.

BASIONYM: *Melobesia minutula* Foslie in *K. nor. Vidensk Selsk. Skr.* **1904** (2): 8 (1904).

NOMENCLATURAL SYNONYM: *Melobesia minutula* f. *lacunosa* Foslie in *K. nor. Vidensk. Selsk. Skr.* **1905** (3): 107 (1905), nom. illeg. (Art. 63.1).

REFERENCES: *Hapalidium callithamnioides* P. Crouan & H. Crouan in *Annls Sci. nat. Bot.* IV, **12**: 289 (1859); Foslie in *K. nor. Vidensk. Selsk. Skr.* **1899** (7): 7 (1900 ['1899']).
Guerinea callithamnioides (P. Crouan & H. Crouan) Picquenard in *Trav. scient. Lab. Zool. Physiol. marit. Concarneau* **4**(3): 1 (1912).
Melobesia callithamnioides sensu Batters in *Grevillea* **21**: 53 (1892).

Table 16 Dimensions of vegetative structures (in μm unless stated).

Pneophyllum confervicolum	British Isles f. *confervicolum*	British Isles f. *minutulum*	Suneson (1943) f. *typica* (= f. *confervicolum*)	Suneson (1943) f. *lacunosum* (= f. *minutulum*)	*Hapalidium callithamnioides* Crouan material
crust diameter	up to 2 mm				
crust depth					
crust cell length	(5·5) 9 (13·5)	(6) 8 (10)	8–12	6–12	(7) 8·5 (10·5)
surface width	(4) 7·5 (14·5)	(6·5) 11 (15·5)	5–9	6–14	(8) 11 (16)
crust cell height	*c.* 10				
epithallial cell length	(1·5) 2·5 (4)	(1·5) 2 (3·5)	very short, lentiform	very short, lentiform	(2) 2·5 (4)
surface view width	(2·5) 5 (8)	(4·5) 6·5 (9)			(6) 7·5 (10)
epithallial cell height					
hypothallial cell width					
VS height					
perithallial width					
cell height					
VS number					
trichocyte type	intrafilament and branch cell				
trichocyte length	as crust cells				
surface view width	as crust cells				

Table 17 Dimensions of reproductive structures (μm unless stated).

Pneophyllum confervicolum	British Isles	Suneson (1943) f. *confervicolum* – as f. *typica* (f. *minutulum* – as f. *lacunosa*)	Ganesan (1963)
CARPOSPORANGIAL CONCEPTACLE			
external diameter			75–120
surface diameter	(57) 62 (65)	75–100 (35–60)	
VS internal diameter	(47) 72 (104)		45–70
VS height	(39) 55 (68)	50–100	40–65
VS roof height	(8) 13 (16)		
roof type	uniform – irregular		
no. basal cell rows	1–2		
ostiole	simple, beaked or filaments	simple or beaked	simple or beaked
no. gonimoblast filaments	*c.* 8.		
diameter carpospore			
SPERMATANGIAL CONCEPTACLE			
VS/surface width	30 (1 only)	(28)	25–40
VS height	23	(18)	25–35
length spermatium			
width spermatium			
TETRASPORANGIAL CONCEPTACLE			
external diameter			(90) 100–120
surface diameter	(67) 75 (91)	85–100 (45–75)	
VS internal diameter	(52) 69 (91)		60–80
VS height	(30) 56 (74)	85–100	50–60
VS roof height	(8) 14 (18)		
roof type	uniform – irregular		
no. basal cell rows	1		
ostiole	simple or beaked		simple
no. tetrasporangia	up to 10	6–12 (3–10)	
length tetrasporangium	(26) 33 (46)		30–35
width tetrasporangium	(15·5) 22 (27·5)		15–20
BISPORANGIAL CONCEPTACLE			
external diameter			
surface diameter		75 (60–90)	
VS internal diameter	(68) 83 (107)		
VS height	(52) 57 (65)	60	
VS roof height	9–10		
roof type	uniform – irregular		
no. basal cell rows	1		
ostiole	simple or beaked		
no. bisporangia		(5–15)	
length bisporangium	(26) 34 (39)		
width bisporangium	(14·5) 18 (21)		

Melobesia minutula f. *lacunosa* Foslie; Suneson in *Acta Univ. lund.* II, **39**: 31 (1943); Feldmann in *Trav. Stn. biol. Roscoff* supplement **6**: 78 (1954); Zinova, *Check-list of green, brown and red algae of the southern seas of the U.S.S.R.*: 232 (1967).
Melobesia minutula sensu Kylin in *Acta Univ. lund.* II, **40**: 56 (1944).
Fosliella minutula f. *lacunosa* (Foslie) Cabioch in *Bull. Soc. phycol. Fr.* **19**: 78 (1974).

HOLOTYPE: TRH! Herb. Foslie, 25 August 1903, south Norway, Hvaløerne 'Galtene' ved Kirkøen c. 5–8 fathoms, on *Corallina officinalis* (Figs 47B; 48A).

DIAGNOSIS: Differing from f. *confervicolum* in having a creeping, filamentous thallus and smaller conceptacles.

DESCRIPTION: With creeping filaments of broad crust cells, *crust cells* 6–10 μm long × 6·5–15·5 μm wide, *epithallial cells* 1·5–3·5 μm long × 4·5–9 μm wide, conceptacles hemispherical.

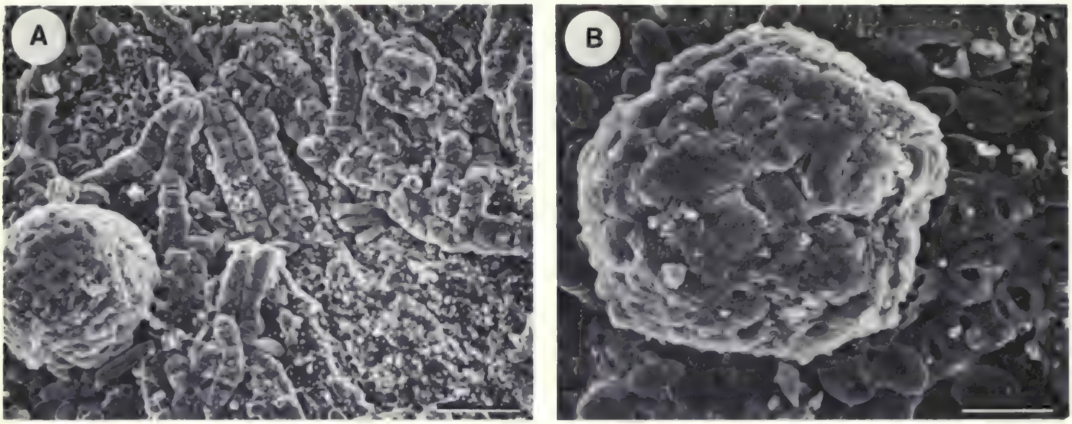


Fig. 47 Scanning electron micrographs of *Pneophyllum confervicolum* f. *minutulum*. A, From Lough Ine. Scale = 50 μm. B, From type specimen of *Melobesia minutula* Foslie (TRH). Scale = 25 μm.

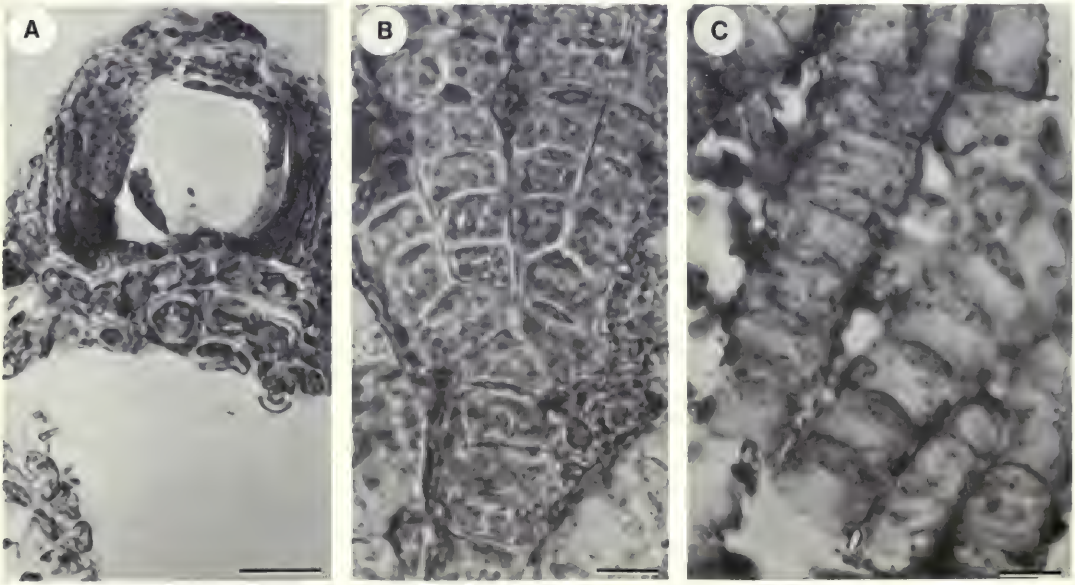


Fig. 48 Features of *Pneophyllum confervicolum* f. *minutulum*. A, Vertical section of conceptacle from type specimen of *Melobesia minutula* Foslie (TRH). Scale = 25 μm. B, Crust growing on *Palmaria palmata* at Bembridge. Scale = 10 μm. C, Crust from type specimen of *Hapalidium callithamnioides* P. Crouan & H. Crouan (CO). Scale = 10 μm.

HISTORICAL: Foslie (1904*b*) described *Melobesia minutula* from Hvalöerne, south Norway, where it grew on *Corallina officinalis*; this was a creeping form (Fig. 47B) which he subsequently (Foslie, 1905*a*) named f. *lacunosa* at the same time applying the epithet f. *typica* to a discoid form found on hydroids from Norway and Denmark. Since the f. *lacunosa* included the type of the species, it should have been called f. *minutula* according to the *International Code* (Art. 26.1). Suneson (1943) described and figured Swedish material of *Melobesia minutula* f. *lacunosa*.

Kylin (1944) correctly restricted *Melobesia minutula* Foslie f. *lacunosa*, but Ganesan (1963) wrongly indicated that this usage was incorrect.

Foslie (1905*a*: 108) included *M. inaequilaterata* Solms-Laub. in the synonymy of *M. minutula* f. *lacunosa*; later (Foslie, 1909, p. 57), he recombined *M. inaequilaterata* in *Heteroderma*, and noted that he considered this synonymous with *Melobesia minutula*. I have not seen Solms-Laubach's material of *M. inaequilaterata* and the description and drawing of young plants (Solms-Laubach, 1881) are not sufficient to enable identification. Other authors (e.g. Mazza, 1922) give it as a synonym of *Fosliella farinosa* (as *Melobesia*).

A further species, described by the Crouan brothers (1859) as *Hapalidium callithamnioides* (see Fig. 44D) appears to be sterile material of *Pneophyllum confervicolum* f. *minutulum*; type material from Concarneau (Fig. 48C) agrees with this form in appearance and cell size (Tab. 16). The material was dredged off Brest and a similarly subtidal collection of f. *minutulum* was reported by Cabioch (1974, as *Fosliella minutula* f. *lacunosa*) growing on maërl at a depth of 45 m off Madeira. Both Foslie (1900*a*) and Picquenard (1912*a*) concluded that the Crouans' material (PC and CO respectively) was not a calcareous alga, but was possibly allied to *Rhodochorton*. However, I found the specimens at Corncarneau to be markedly calcified and composed of broad crust cells bearing epithallial cells (Fig. 48C) which Foslie (1900*a*) and Picquenard (1912*a*) had thought to be absent. Picquenard (1912*a*) proposed a new genus, *Guerinea*, to accommodate this species.

CRUST APPEARANCE: The thallus of f. *minutulum* forms filaments (Fig. 20B) which creep, often for considerable distances, over other algae and sea-grasses; Foslie (1905*a*) and Suneson (1943) describe plants growing on *Corallina* and *Jania*. The filaments usually produce rather fewer conceptacles than the crusts of f. *confervicolum*.

VEGETATIVE ANATOMY: The cells of f. *minutulum* (Fig. 48B) are usually considerably broader than wide, with very broad, short epithallial cells; these features are also apparent in the type material of *Hapalidium callithamnioides* (Fig. 48C).

CONCEPTACLES: Few conceptacles have been observed in the present investigation. In general, however, they are similar to but smaller than those of f. *confervicolum*. Suneson (1943, p. 32) shows adjacent carpogonial and spermatangial conceptacles.

PHENOLOGY: Forma *minutulum* has been recorded from May to November in the present investigation.

DISTRIBUTION:
British Isles: Hampshire, Dorset, Anglesey, Co. Cork, Co. Galway, Co. Clare.
World: Sweden, France, Madeira, southern U.S.S.R.

6. Pneophyllum microsporum (Rosenv.) Y. Chamberlain, **comb. nov.**

BASIONYM: *Melobesia microspora* Rosenv. in *K. danske Vidensk. Selsk. Skr.* VII, **7**: 256 (1917).

HOLOTYPE: C! Herb. Rosenvinge no. 4670, 23 April 1894, Ryes Flak, Denmark, 2–5 fathoms, on *Furcellaria lumbricalis* (Fig. 49A).

DIAGNOSIS: Epiphyte with deep, crumbly crust up to 14 cells deep and immersed conceptacles with a simple ostiole: differing from *P. sargassi* in having uniform conceptacle surface, from *P. plurivalidum* in not having domed ostiole, from *P. concollum* in not having an ostiolar collar and in having fewer sporangia and smaller conceptacles, from *P. lejolisii* in having a deep perithallium and from *P. confervicolum* in having flat conceptacles and a deep perithallium.

DESCRIPTION: Deep, heavily calcified, crumbly, brownish-pink crusts up to 5 mm diameter, 140 μm deep, perithallium up to 14 cells deep in crust centre, one to a few cells deep at periphery, *perithallial cells* (in VS) 5–14 μm wide × 5–21 μm high; *crust cells* in surface view square to somewhat elongate, 5–13·5 μm long × 4·5–12 μm wide; intrafilament and branch cell *trichocytes* of same size range as crust cells; conceptacles immersed, all except spermatangial conceptacles with simple ostiole, *carposporangial conceptacles* 45–104 μm internal diameter × 33–78 μm high, *spermatangial conceptacles* 15–49 μm wide × 23–34 μm high, ostiole prolonged into a spout, *tetrasporangial conceptacles* 54–130 μm internal diameter × 49–70 μm high, 6–12 peripheral tetrasporangia per conceptacle, 22–48 μm long × 18–29 μm wide, central sterile paraphyses sometimes evident, *bisporangial conceptacles* 62–98 μm internal diameter × 42–63 μm wide, 3–8 peripheral bisporangia per conceptacle, 25–38 μm long × 19·5–29 μm wide, central sterile paraphyses present.

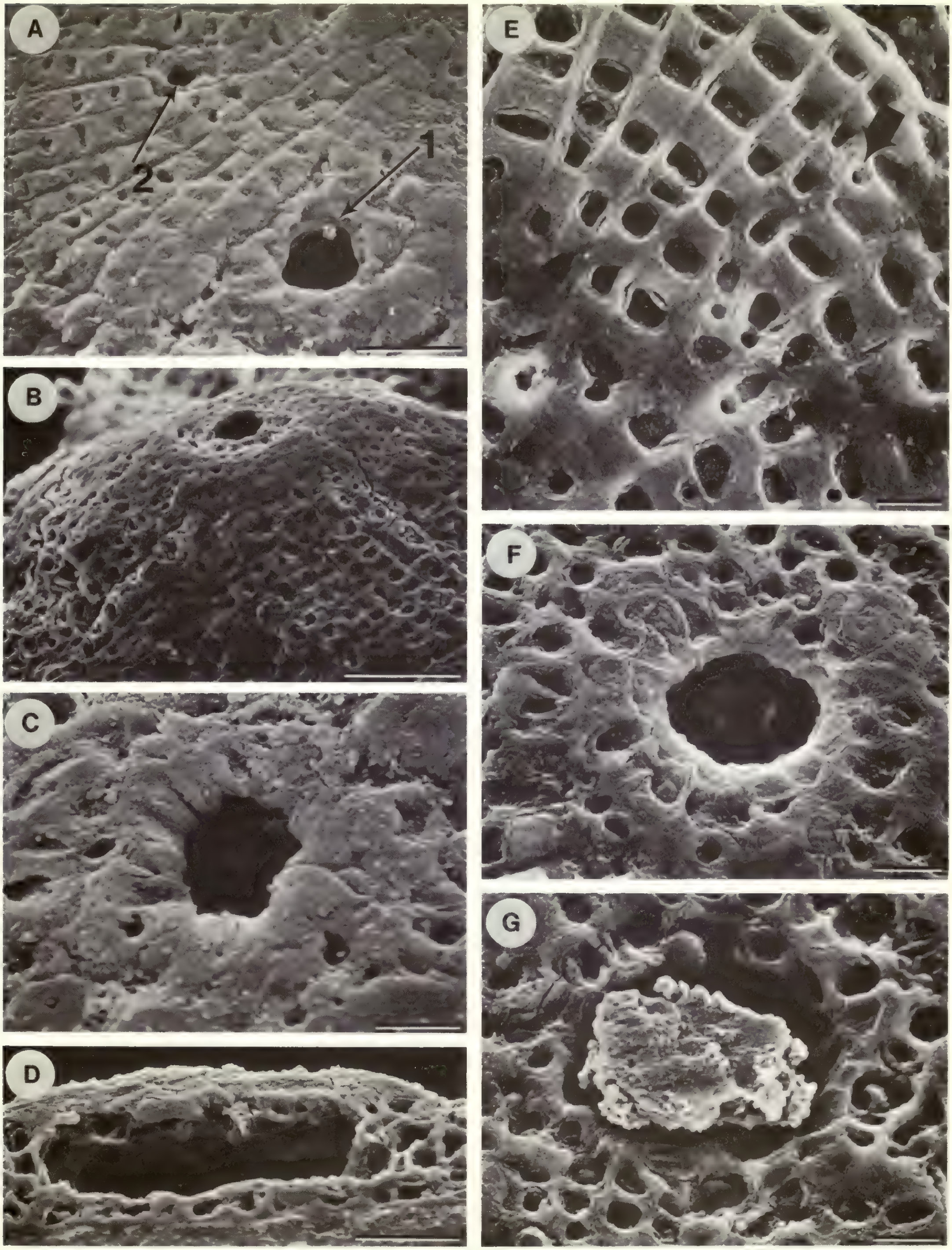
HISTORICAL: *P. microsporum* was described by Rosenvinge (1917) as an epiphyte growing on *Furcellaria lumbricalis* in Denmark. It was characterised by having perithallial filaments up to 5 cells deep, very small tetrasporangia, and no epithallial cells. Examination of the type material under the S.E.M. (Fig. 49A) and decalcified whole mounts, however, show that short, wide epithallial cells are present, while the tetrasporangia on slides made by Rosenvinge appear to be young; mature ones would probably be larger than the dimensions of 17–24 μm long × (9) 11–12 (16) μm wide recorded by Rosenvinge (1917).

P. microsporum has not been recorded since 1917, but an entity found commonly in southern England and south-west Ireland is now referred to this species; although crusts occur quite frequently they are rather inconspicuous and difficult to characterise, which no doubt accounts for the previous lack of records. The principal difference between Rosenvinge's material and that from the British Isles lies in the appearance of the crust cells under the S.E.M. Rosenvinge's material (Fig. 49A) has broad but very short epithallial concavities, while these are relatively longer in material from the British Isles (Fig. 49E). Decalcified crusts from the British Isles, however, have short, wide epithallial cells (Fig. 50) similar to those observed on Rosenvinge's material.

CRUST APPEARANCE: This species forms thick, heavily calcified crusts (up to 140 μm deep) which crumble and detach easily. It grows epiphytically on a number of algal species, most frequently on *Furcellaria lumbricalis* (as did the type) and *Chondrus crispus*. The crusts are deep pink or brownish-pink and often have a somewhat granular, glistening appearance; they are irregularly shaped and measure up to about 3 mm diameter on *Furcellaria* and 5 mm on *Chondrus*. The small crowded conceptacles (Figs 49B–D) are scarcely raised; when old they often become very pale and form conspicuous circles on the darker crust.

Under the S.E.M. (Fig. 49E) the crust cells vary from square to elongate with conspicuous epithallial concavities which are shorter than wide. The crust edge is thick since perithallial filaments usually start to develop immediately behind the first meristem. Intercalary trichocytes occur only very occasionally in English material, possibly because it grows there mainly in winter; they are abundant, however, on material collected in Ireland in May (Fig. 49E). The conceptacles have a uniform surface often with a smooth covering in the ostiole area (Figs 49B, C). The ostiole is small and simple when young (Figs 49B, C), but the edges cave in to produce a large hole in old conceptacles (Figs 49F, G).

Fig. 49 Scanning electron micrographs of *Pneophyllum microsporum* from various localities. A, Type specimen of *Melobesia microspora* Rosenv. (Ryes Flak, Denmark, April 1894) showing carposporangial (1) and spermatangial (2) ostiole. Scale = 25 μm. B, Side view of conceptacle (Bembridge, 13 January 1979). Scale = 50 μm. C, Ostiole from same crust as B (Bembridge, 3 January 1979). Scale = 10 μm. D, Vertical section of conceptacle (Bembridge, 13 January 1979). Scale = 25 μm. E, Crust periphery with trichocytes (arrow) (Finavarra, 3 May 1981). Scale = 10 μm. F, Mature ostiole (Finavarra, 3 May 1981). Scale = 10 μm. G, Senescent ostiole (Finavarra, 3 May 1981). Scale = 10 μm.


A
1
2
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Vegetative anatomy: In surface view (Fig. 50) the crust cells vary from almost square to somewhat elongate, and the epithallial cells are relatively short and wide. The intercalary trichocytes are mainly intrafilament but occasionally occur in branch cells; they are the same size as normal crust cells.

In vertical section (e.g. Figs 51; 52A; 54B) the crusts are composed of regular, mainly almost isodiametric perithallial cells; the perithallial filaments may be up to 13 cells deep and are usually initiated at, or near, the crust periphery.

Gametangial plants: Gametangial plants are monoecious, the spermatangial conceptacles (Figs 49A; 51A; 52C) are adjacent to the carpogonial conceptacle, they are completely immersed and have a spout (Figs 51C; 52D).

Carpogonial conceptacles are immersed and bear procarps in a bunch in the centre of the conceptacle floor (Figs 52A, B; 54A), but the conceptacles are so small that their structure has not been fully elucidated. In material from Ireland the crusts are very deep, there are usually two or three cells below the conceptacle base, and the conceptacles appear entirely flat in surface view (Figs 51A). This is sometimes the case in English material but conceptacles may also be initiated on thinner, peripheral parts of the crust in which case they have only a single basal cell layer and may appear raised.

Carposporangial conceptacles: The mature conceptacle is either entirely immersed, as in Irish and some English material (Figs 51A; 54B), or somewhat raised as in other English material (Fig. 51B). The roof is composed of small, irregular filaments, and the ostiole is simple externally but with some development of the downward filaments (Fig. 51A). The small fusion cell bears carposporangial filaments up to seven cells long from the periphery

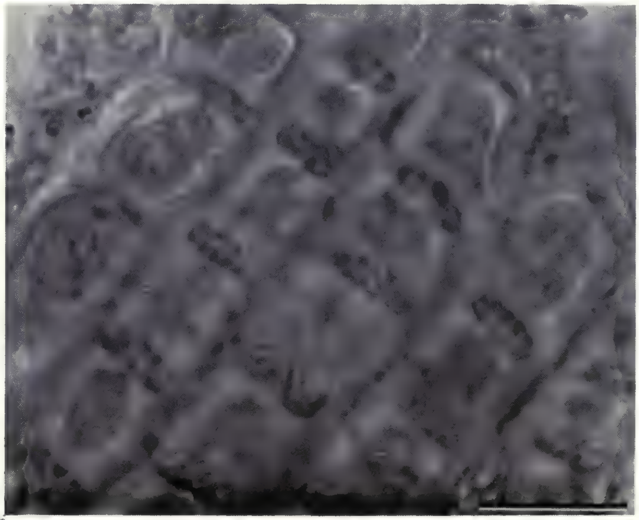

Fig. 50 Surface view of decalcified crust of *Pneophyllum microsporum*. Scale = 10 μm.

Tetrasporangial plants: The shape, size, and ostiole structure of tetrasporangial conceptacles (Figs 53A; 54E, F) are similar to the carposporangial conceptacles. The farctate sporangia are borne peripherally, and there is some development of central, sterile paraphyses. The sporangia are not particularly small in relation to the conceptacle; the small dimensions given by Rosenvinge (1917), after which the species is named, were probably obtained from immature sporangia.

Bisporangial plants: These are similar to the tetrasporangial plants and likewise have central sterile paraphyses (Figs 53B; 54C, D). The bisporangial plants may be difficult to distinguish from the small type bisporangial form of *P. limitatum* found in the British Isles.

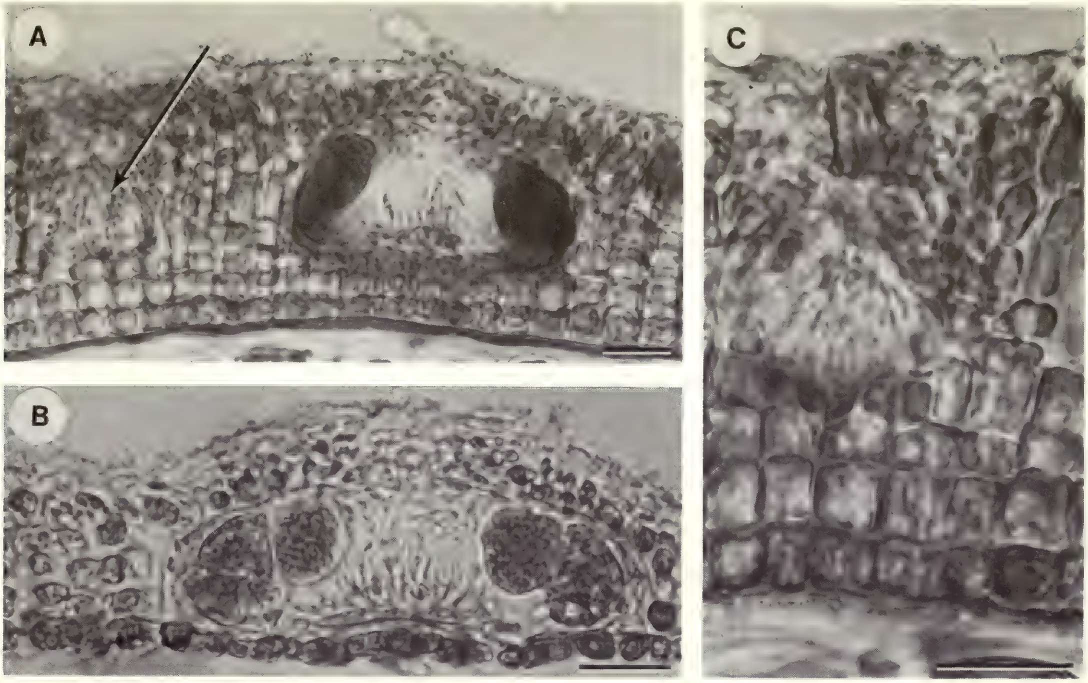

Fig. 51 Gametangial/carposporangial conceptacles of *Pneophyllum microsporum*. A, Vertical section of carposporangial and spermatangial (arrow) conceptacles from Finavarra, Co. Clare. Scale = 25 μm. B, Vertical section of carposporangial conceptacle from Bembridge. Scale = 25 μm. C, Vertical section of spermatangial conceptacle from Finavarra. Scale = 20 μm.

PHENOLOGY: Apart from sporadic records in other parts of southern England, Ireland, and France, the principal population of *P. microsporum* investigated was that at Bembridge where the species is present mainly during the winter and is most abundant at this time on *Chondrus crispus* (Chamberlain, 1982). Otherwise the principal host is *Furcellaria lumbricalis* and samples were collected at all times of year. All the Irish material was collected in May and no winter collections are available for comparison.

FORM RANGE: There are considerable differences in the structure and appearance of *P. microsporum* from Ireland and that mostly seen in England. The Irish plants have a deep thallus with the conceptacles situated near the surface; the conceptacles are noticeably larger than in the English material, tetrasporangial conceptacles, for example, measure 54–99 μm internal diameter in English plants and 117–130 μm in Irish plants. In addition the English plants often have somewhat raised conceptacles (Fig. 49B) among which much detritus collects, while the Irish plants have completely flat conceptacles externally.

English material may also have flat conceptacles and very deep thalli, but the predominance of the larger form in Ireland suggests a geographical variation.

DISTRIBUTION:
British Isles: Hampshire, Dorset, Devon, Mull, Channel Islands, Co. Galway, Co. Clare, Co. Down.
World: Denmark, France.

Insufficient data are available to assess the distribution range of *P. microsporum*. On present evidence it would appear to be restricted to northern Europe.

HABITAT: Epiphytic on the following algae: *Furcellaria lumbricalis, Polyides rotundus* (once only), *Phyllophora crispa, P. pseudoceranoides, Chondrus crispus, Palmaria palmata, Gastroc-*

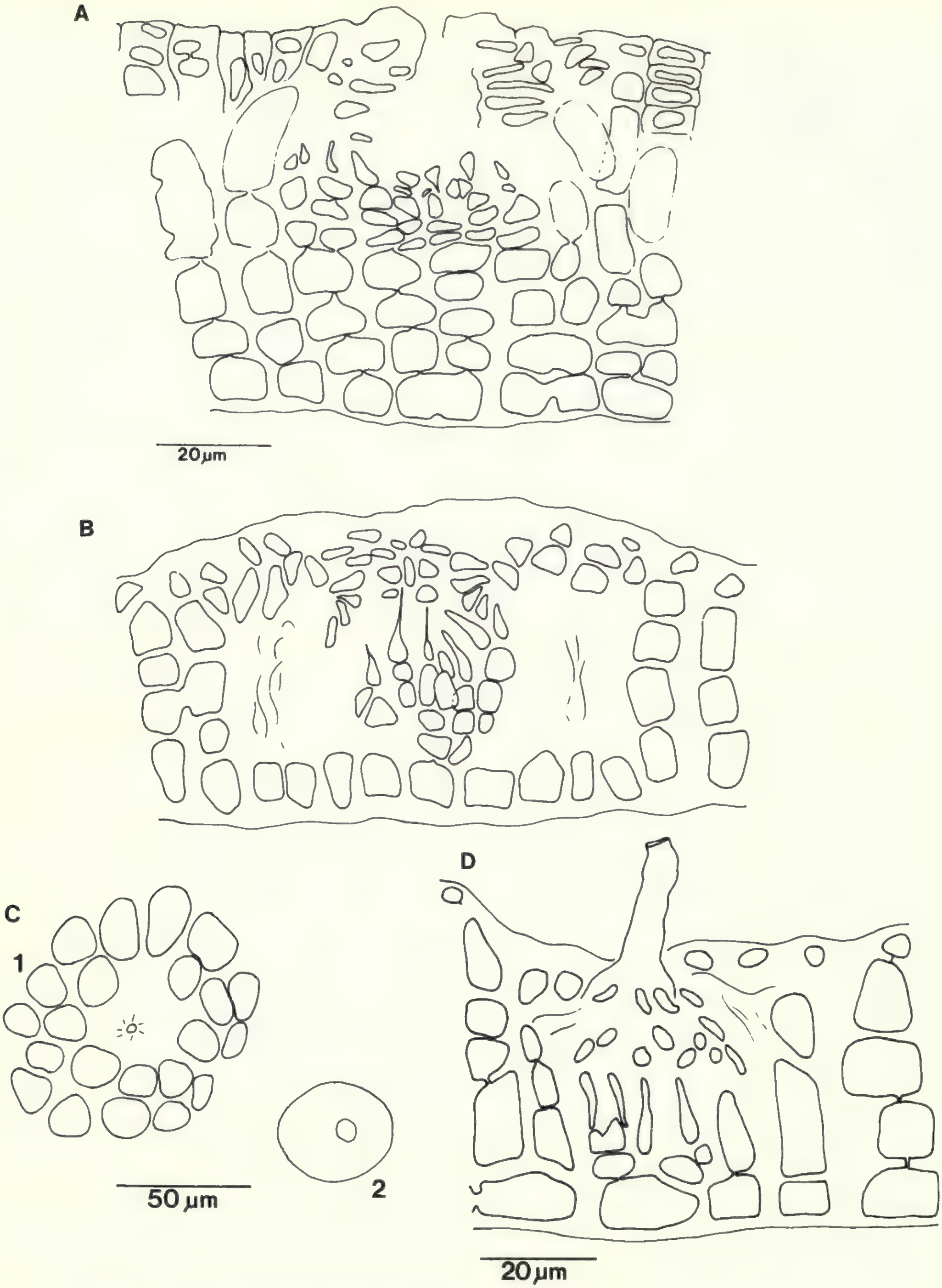

Fig. 52 Carpogonial/carposporangial and spermatangial conceptacles of *Pneophyllum microsporum* from Bembridge and Ireland. A, Vertical section of young carpogonial conceptacle (Ireland). B, Vertical section of carpogonial conceptacle (Bembridge). C, Surface view carposporangial (1) and spermatangial (2) conceptacles (Bembridge). D, Vertical section of spermatangial conceptacle (Bembridge).

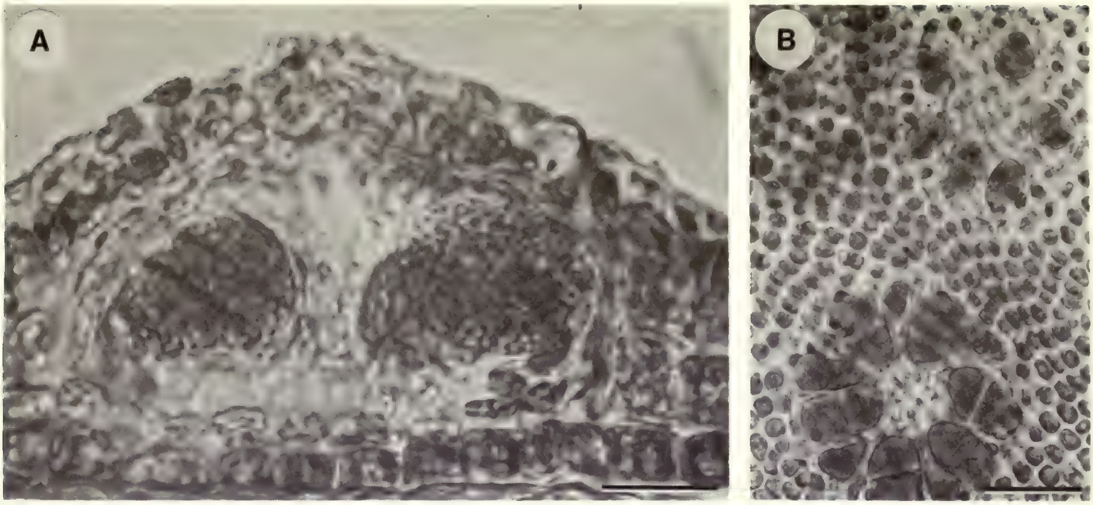

Fig. 53 Tetra/bisporangial conceptacles of *Pneophyllum microsporum*. A, Vertical section of tetrasporangial conceptacle from Bembridge. Scale = 20 μm. B, Surface view of bisporangial conceptacles from Bembridge. Scale = 50 μm.

lonium ovatum, Halopitys incurvus, Laurencia pinnatifida, Polysiphonia elongata, Laminaria digitata, Fucus serratus, Cystoseira nodicaulis, Sargassum muticum.

The hosts on which *Pneophyllum microsporum* are most commonly found are *Chondrus crispus* on which it may form extensive, brownish-pink colonies and *Furcellaria lumbricalis* on which it is frequent but usually in scattered individual crusts.

Table 18 Dimensions of vegetative structures (in μm unless stated).

Pneophyllum microsporum	British Isles	Rosenvinge (1917)
crust diameter	up to 5 mm	1–2 mm
crust depth	up to 140	
crust cell length	(5) 8·5 (13·5)	
surface width	(4·5) 8·5 (12)	
crust cell height	*c.* 8	
epithallial cell length	(1·5) 3 (4·5)	
surface view width	(4) 5·5 (8·5)	
epithallial cell height	3–6	
hypothallial cell width	(5) 9·5 (15)	5–8
VS height	(5) 8·5 (12·5)	*c.* 5–8
perithallial width	(5) 11 (14)	6–8
cell height	(5) 12 (21)	6–16
VS number	up to 14 cells	up to 6 cells
trichocyte type	intrafilament (few branch cell)	
trichocyte length	as crust cells	
surface view width	as crust cells	

RIDGWAY COLOUR CODE: dry crust – brownish vinaceous
fresh crust – pale brownish vinaceous

Table 19 Dimensions of reproductive structures (μm unless stated).

Pneophyllum microsporum	British Isles	Rosenvinge (1917)
CARPOSPORANGIAL CONCEPTACLE		
external diameter		120–140
surface diameter	(58) 87 (102)	
VS internal diameter	(45) 86 (104)	
VS height	(33) 54 (78)	
VS roof height	(7) 18 (31)	
roof type	uniform	uniform
no. basal cell rows	1–4	
ostiole	simple	simple
no. gonimoblast filaments	8–14+	
diameter carpospore		
SPERMATANGIAL CONCEPTACLE		
VS/surface width	(15) 38 (49)	*c.* 40
VS height	(23) 29 (34)	
length spermatium	3·5–5·5	6
width spermatium	2–3	2
TETRASPORANGIAL CONCEPTACLE		
external diameter		120–140
surface diameter		
VS internal diameter	(54) 103 (130)	70–110
VS height	(49) 60 (70)	
VS roof height	(13) 23 (31)	
roof type	uniform	uniform
no. basal cell rows	1–5	1–4
ostiole	simple	
no. tetrasporangia	6–12	
length tetrasporangium	(22) 37 (48)	17–24
width tetrasporangium	(18) 23 (29)	(9) 11–12 (16)
BISPORANGIAL CONCEPTACLE		
external diameter		
surface diameter	(39) 76 (117)	
VS internal diameter	(63) 80 (98)	
VS height	(42) 54 (63)	
VS roof height	(12) 17 (20)	
roof type	uniform	
no. basal cell rows	1–3	
ostiole	simple	
no. bisporangia	3–8	
length bisporangium	(25) 32·5 (38)	
width bisporangium	(19·5) 24 (29)	

7. Pneophyllum concollum Y. Chamberlain, sp. nov.

REFERENCES: *Melobesia rosea* sensu Rosanoff in *Mem. Soc. imp. Sci. nat. Cherbourg* **12**: 77 Pl. II, Figs 1, 2 (1866), non *Hapalidium roseolum* Kütz. (See Fig. 3 of present study).

Melobesia lejolisii Rosanoff pro parte in *Mem. Soc. imp. Sci. nat. Cherbourg* **12**: Pl. I, Figs 8, 9 only (1866). (See Fig. 2 and p. 305 of present study.)

HOLOTYPE: BM! Y. M. Chamberlain no. 76/100, 4 April 1976, Ballyandreen, Co. Cork, southern Ireland, growing on *Laurencia pinnatifida* coll. M. D. Guiry (Fig. 55A).

DIAGNOSIS: Species epiphytica, filamentis perithallis profunditate usque ad 8 cellulas et ostiolis ad instar colli; a *P. rosanoffii* differt filamentis ostiolaribus libris carentibus, a *P. sargassi* et *P. microsporo* ostiolis ad instar colli, et a *P. myriocarpo* (specie epilithica) perithallio profundo.

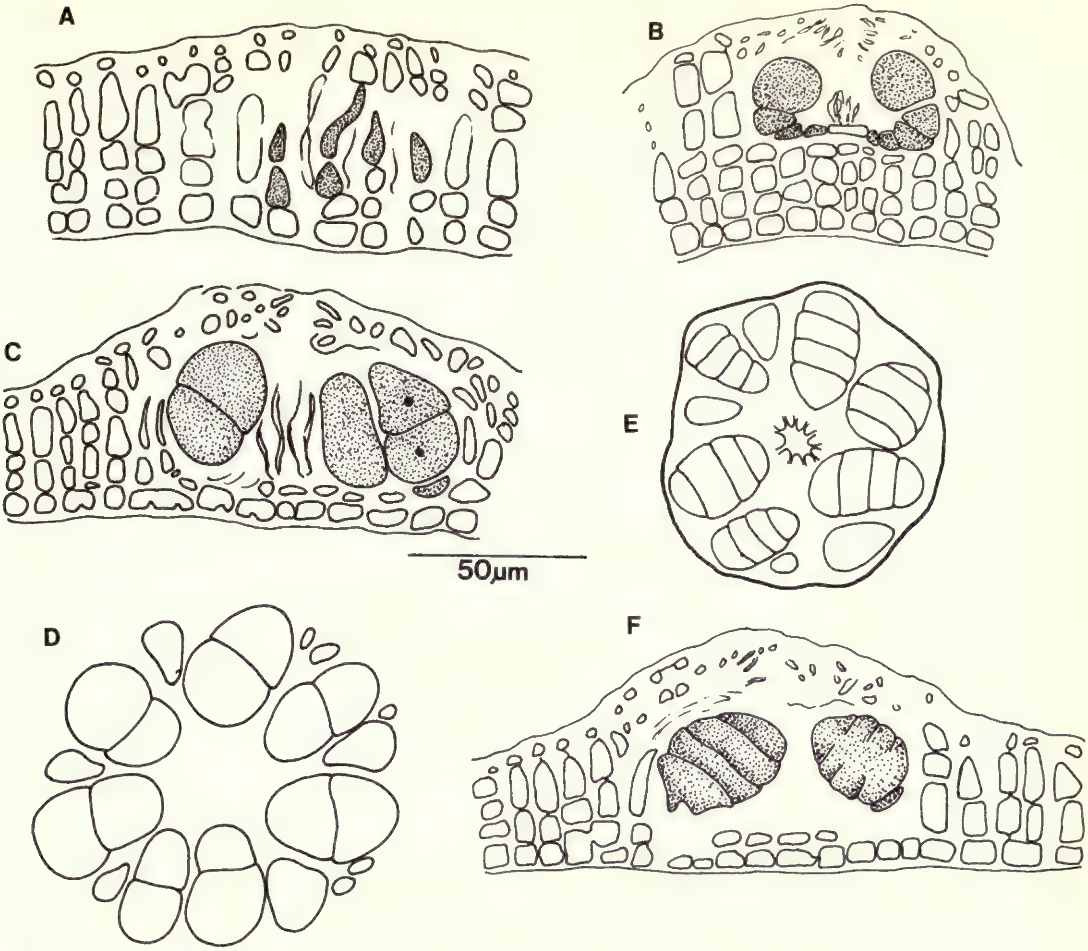

Fig. 54 Reproductive crusts of *Pneophyllum microsporum* from Bembridge. A, Vertical section of very young carpogonial conceptacle. B, Vertical section of mature carposporangial conceptacle. C, Vertical section of mature bisporangial conceptacle. D, Surface view of mature bisporangial conceptacle. E, Surface view of mature tetrasporangial conceptacle. F, Vertical section of mature tetrasporangial conceptacle.

Description: Crustae leaves, malvinae, diametro usque at 5 mm, profunditate 75 µm, lobis parum superpositis; perithallium media in crusta profunditate usque ad 8 cellula, ad marginem carens vel profunditate 1–4 cellularum, *cellulae perithallii* (in sectione verticali) 6·5–14·5 µm latae × 4·5–28·5 µm altae, *cellulae crustae* aspectu superficiali rectangulares, 6·5–22·5 µm longae × 4–15·5 µm latae, cellulae epithallii 3–6·5 µm longae × 3–8 µm latae, *trichocyti* non visi; conceptacula immersa vel parum elevata, omnia, praeter ea spermatangialia, ostiolo ad instar colli, nonnumquam canale superimposito, *conceptacula carposporangialia* diametro interno 91–156 µm, altitudine 52–83 µm, cellula conjungens lata et tenuis, *conceptacula spermatangialia* immersa, 20–65 µm lata × 19–37 µm alta, ostiolo in canalem producto, *conceptacula tetrasporangialia* diametro interno 104–208 µm, altitudine 39–104 µm, 16–20 tetrasporangiis in unoquoque conceptaculo, tetrasporangia 30–65 µm longa × 18–41 µm lata, paraphyses centrales steriles adsunt, *conceptacula bisporangialia* diametro interno 104–182 µm, altitudine 52–104 µm, 16–20 bisporangiis in unoquoque conceptacula, bisporangia 33·5–52 µm longa × 15·5–42 µm lata, paraphyses centrales steriles conspicuae.

Diagnosis: Epiphytic species with perithallial filaments up to 8 cells deep and collar-like ostiole: differing from *P. rosanoffii* in not having free ostiolar filaments; from *P. sargassi* and *P.*

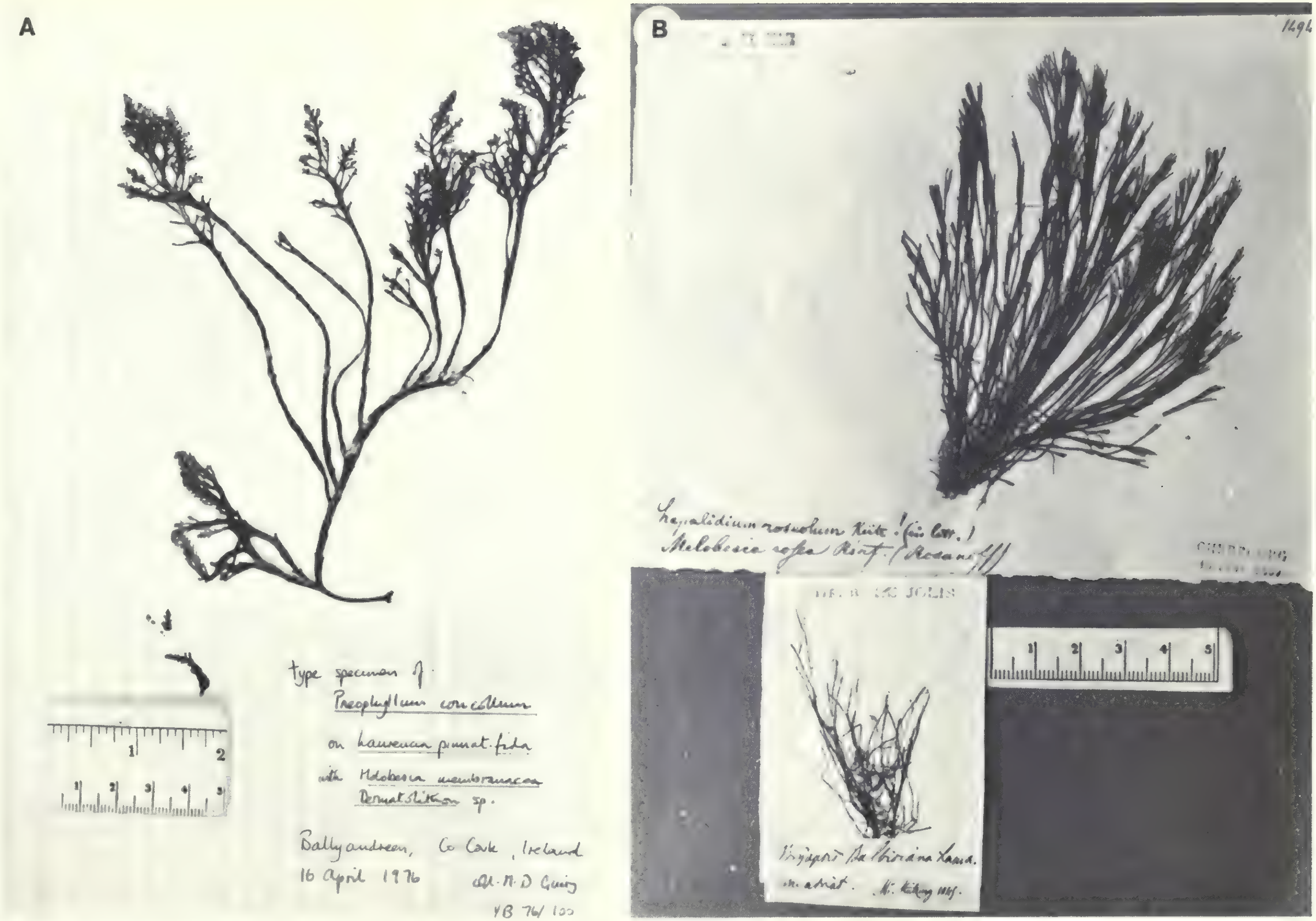
A
type specimen of
Pneophyllum concollum
on Laurencia pinnatifida
with Melobesia membranacea
Dermatolithon sp.
Ballyandreen, Co Cork, Ireland
16 April 1976
coll. M. D Guiry
YB 76/100
1
2
B
1494
Hapalidium roseolum Kütz.! (in litt.)
Melobesia rosea Rsnf. (Rosanoff)
HERB. LE JOLIS
Bryopsis Balbisiana Lamour.
M. adriat. Mr Kützing 1849.
1
2
3
4
5

Fig. 55 Type specimens of *Melobesia rosea* Rosanoff and *Pneophyllum concollum*. A, Holotype of *Pneophyllum concollum* (BM). B, *Upper specimen* – lectotype of *Melobesia rosea* Rosanoff ex Herb. Le Jolis (CHE) (in *Melobesia membranacea* folder); *Hapalidium roseolum* Kütz.! (in litt.) in Rosanoff's hand; *Melobesia rosea* Rsnf. (Rosanoff) in Le Jolis's hand. *Lower specimen* – *Hapalidium roseolum* Kützing (CHE); *Bryopsis Balbisiana* Lamour. M adriat. in Kützing's hand; Mr Kützing 1849 in Le Jolis's hand.

microsporum in having a collar-like ostiole, and from *P. myriocarpum* (epilithic) in having a deep perithallium.

DESCRIPTION: Smooth, mauvy-pink crusts up to 5 mm diameter, 75 μm deep, with slightly overlapping lobes, perithallium up to 8 cells deep in crust centre, absent or 1–4 cells deep at periphery, *perithallial cells* (in VS) 6·5–14·5 μm × 4·5–28·5 μm high; *crust cells* in surface view rectangular, 6·5–22·5 μm long × 4–15·5 μm wide, *epithallial cells* 3–6·5 μm long × 3–8 μm wide, *trichocytes* not seen; conceptacles immersed or somewhat raised, all except spermatangial conceptacles with collar-like ostiole sometimes surmounted by a spout, *carposporangial conceptacles* 91–156 μm internal diameter × 52–83 μm high, fusion cell wide and thin, *spermatangial conceptacles* immersed, 20–65 μm wide × 19–37 μm high, ostiole prolonged into a spout, *tetrasporangial conceptacles* 104–208 μm internal diameter × 39–104 μm high, 16–20 tetrasporangia per conceptacle, 30–65 μm long × 18–41 μm wide, central sterile paraphyses present, *bisporangial conceptacles* 104–182 μm internal diameter × 52–104 μm high, 16–20 bisporangia per conceptacle, 33·5–52 μm long × 15·5–42 μm wide, central sterile paraphyses pronounced.

HISTORICAL: The identity of *P. concollum* has only become clear during a prolonged study of *Pneophyllum* species in the British Isles. It is characterised by the collar-like ostiole, somewhat developed perithallium, and frequent presence of balloon-like paraphyses in the tetra- and bisporangial conceptacles. None of these characters is very conspicuous, however, and the ostiole structure, which is the most clearly diagnostic character, may easily be missed in sectioning. For these reasons the taxon has not previously been distinguished, although it is now clear that it is the taxon which Rosanoff (1866), with some hesitation, described as *Melobesia rosea* growing on *Bornetia secundiflora* (J. Agardh) Thuret at Cherbourg (Fig. 55B). The material in Le Jolis's herbarium (CHE) on which Rosanoff's description is based agrees in surface features and ostiole structure with the present taxon. In addition I believe that material of *Pneophyllum concollum* was included originally by Rosanoff (1866) in his concept of *Melobesia lejolisii*. It was on this material that Rosanoff did his conceptacle drawing shown in Figures 2 [8, 9] of the present study, and on which his record of *M. lejolisii* growing on *Bornetia,* was based. Since no *Bornetia* specimens are now present in the folders of *Melobesia lejolisii* (CHE) it seems that Rosanoff later changed his mind about this material and transferred it to *M. rosea*. Further discussion of Rosanoff's concept of *Pneophyllum concollum* is given on pages 306–308.

CRUST APPEARANCE: The mauvy-pink crusts appear opaque but rather thin (up to 75 μm deep). They may have a spotted appearance and the surface is usually cracked in dried material. The plants are epiphytic on algae and are characteristically composed of a number of slightly overlapping crusts (Fig. 56A). It is not usually possible to measure individual crusts, but they probably do not attain more than 5 mm diameter.

Under the S.E.M. (Fig. 56D) the crust cells are regularly rectangular and the epithallial concavities vary from rounded rectangular to short and broad; trichocytes have not been seen.

In fresh material the conceptacles appear almost flat while in dried material they are somewhat rounded. Under the S.E.M. they mostly have a uniform surface (Figs 56A–C) which may be covered with a smooth coating (Fig. 56C) which is probably mucilaginous; in critical point dried material (Fig. 56B) the smooth surface may crack irregularly to reveal the newly developed roof cells. Under the S.E.M. the ostiole is mostly simple (Figs 56B, C) or surrounded by a small collar.

VEGETATIVE ANATOMY: The crusts may have an extended margin composed of hypothallium and epithallium only or may initiate perithallial filaments immediately behind the periphery. In surface view (Fig. 57B) the crust cells are regularly rectangular; the size varies considerably both within and between crusts. Plastids are plentiful and conspicuous but starch grains are not evident. The epithallial cells vary from rounded rectangular to short and broad, and are dome-shaped or flattened in VS.

In VS (e.g. Figs 59B; 60B) the crusts appear rather regularly zoned horizontally; the

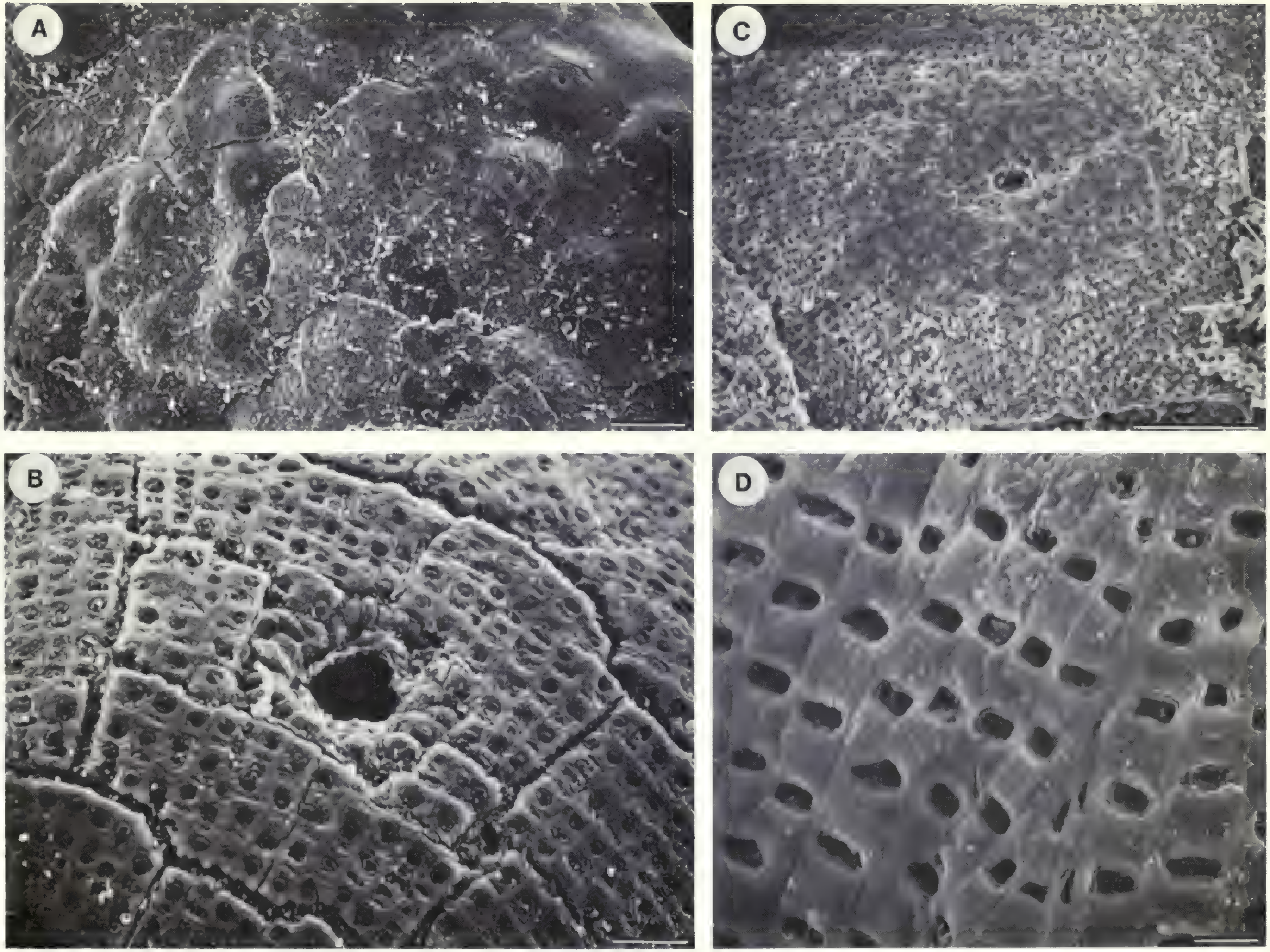

Fig. 56 Scanning electron micrographs of *Pneophyllum concollum*. A, General view of critical point dried crusts from Ballyandreen (type). Scale = 250 μm. B, Ostiole from A. Scale = 25 μm. C, Conceptacle surface from Ballyandreen. Scale = 100 μm. D, Crust cells from Lundy. Scale = 10 μm.

perithallial filaments vary from 1–8 cells deep and their cells vary from short to very elongated, the uppermost cell (subapical initial) often markedly tapers upward.

GAMETANGIAL PLANTS: Gametangial plants are monoecious. The spermatangial conceptacles, which are usually adjacent to the carpogonial conceptacles, are relatively broad and shallow (Figs 57C; 58B). They are completely immersed and have a spout.

Carpogonial conceptacles are usually gently raised (Fig. 58A), with the fertile disc being surrounded by a wide ring of stretched perithallial cells. There are from 1–4 rows of cells below the conceptacle base and the procarps bear one or two carpogonia (Fig. 58A). In some populations such as that at Beer, south Devon, the carpogonial conceptacles are narrower and more abruptly dome-shaped.

CARPOSPORANGIAL CONCEPTACLES: The mature conceptacle is somewhat raised (Figs 57A; 58C, D), the roof is quite deep, and there are 1–4 cell rows below the conceptacle. The ostiole is surrounded by filaments which are united laterally to form a collar (Fig. 57D), and sometimes this is surmounted by a spout (Figs 57A; 58D) similar to that seen in the spermatangial conceptacle; the downward ostiolar filaments are well developed and may become balloon-like. The fusion cell is characteristically wide and very thin (Figs 58C, D), and the gonimoblast filaments, which are produced peripherally, are usually seven cells long.

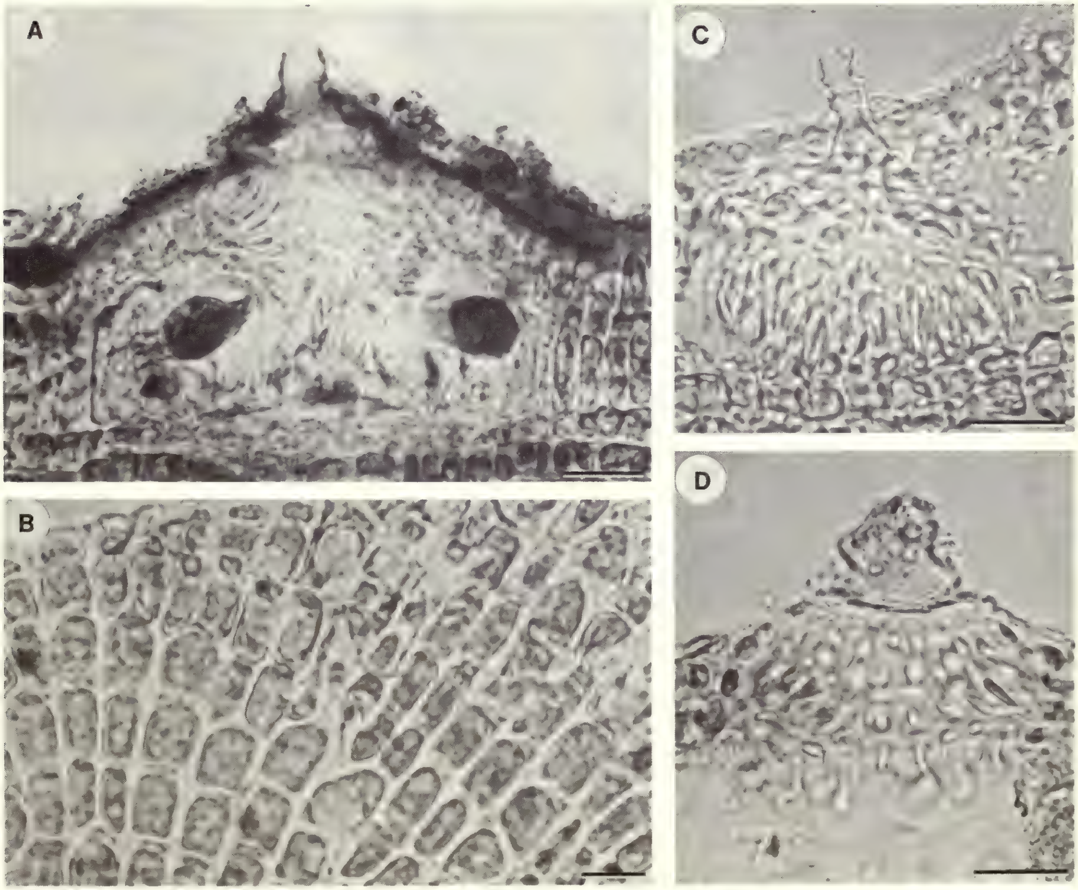

Fig. 57 Features of *Pneophyllum concollum*. A, Vertical section of carposporangial conceptacle from Beer. Scale = 25 μm. B, Crust cells in surface view. Scale = 10 μm. C, Vertical section of spermatangial conceptacle from Ballyandreen. Scale = 20 μm. D, Characteristic collar-like ostiole. Scale = 20 μm.

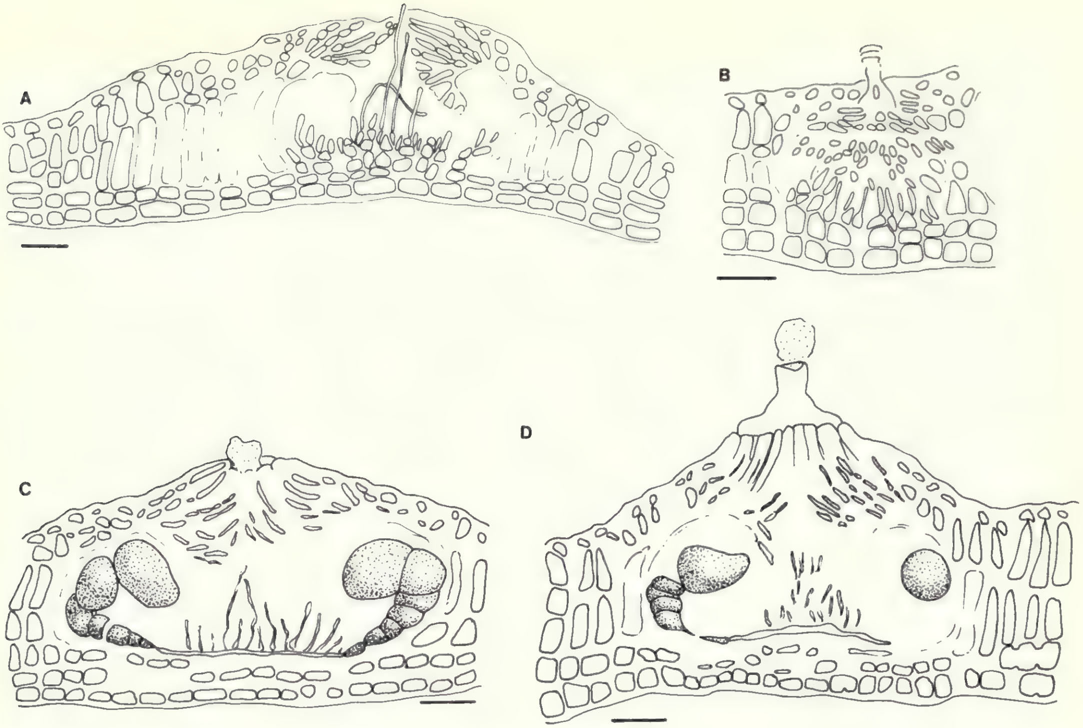

Fig. 58 Vertical sections of gametangial crusts of *Pneophyllum concollum*. A, Carpogonial conceptacle. B, Spermatangial conceptacle. C, Carposporangial conceptacle with ostiole collar. D, Carposporangial conceptacle with ostiole prolonged into a spout. Scale = 20 μm (all figures).

TETRASPORANGIAL PLANTS: Conceptacle shape and ostiole structure (Figs 59A; 60A, B) are similar to that seen in the carposporangial conceptacle. The tetrasporangia are borne peripherally, they remain pigmented and farctate throughout development, and are not invaginated. The mature sporangia are rather small in relation to the size of the mature conceptacle and appear as a peripheral ring in surface view; sterile cells develop centrally on the conceptacle base (Figs 59A; 60B) to form a columella and these cells may become balloon-like.

BISPORANGIAL PLANTS: The development and structure of bisporangial conceptacles (Figs 59B; 60C–E) is the same as for tetrasporangial conceptacles. The bisporangia are even smaller in relation to conceptacle size than the tetrasporangia. The central sterile filaments and downward ostiolar filaments may be balloon-like (Fig. 60E) in bisporangial as in tetrasporangial plants.

PHENOLOGY: Insufficient evidence is available to generalise on the seasonal periodicity of *P. concollum*. At present it is known that at Beer, south Devon the species occurs in the intertidal zone only in winter (October–April) and the intertidal records from Wembury (south Devon) are also mainly of winter material. In the subtidal, however, *P. concollum* is abundant in July at Lundy Island and the Scilly Isles. In southern and western Ireland the species is common in both intertidal and subtidal habitats from April to August but no records are yet available for the winter months. All reproductive phases occur at the different localities.

Le Jolis's samples on *Bornetia* are in excellent condition; both were collected in February (1857 and 1859) which suggests that in that locality, on that host, this was the optimum season.

The indications are, therefore, that *Pneophyllum concollum* is able to grow throughout the year except in very cold conditions, but that its actual occurrence depends on local circumstances.

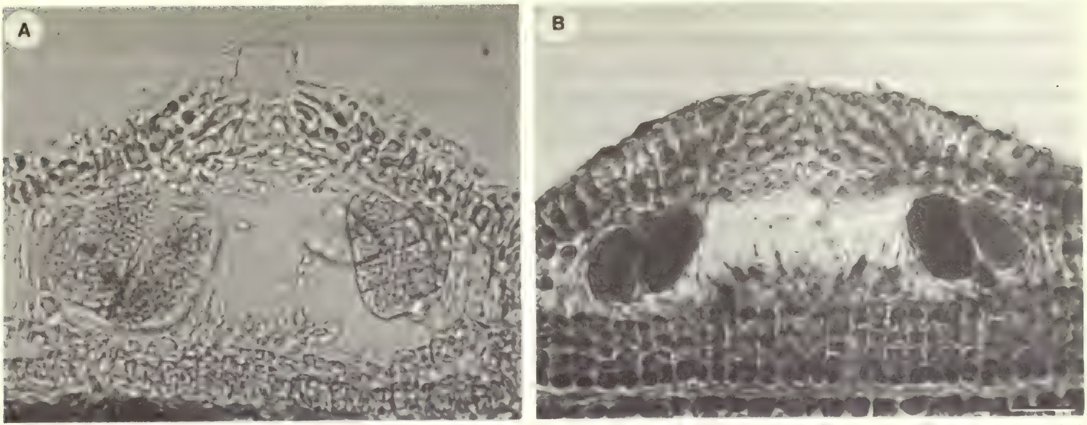

Fig. 59 Vertical sections of sporangial conceptacles of *Pneophyllum concollum*. A, Tetrasporangial conceptacle from Ballyandreen. B, Bisporangial conceptacle from Wembury. Scale = 25 μm.

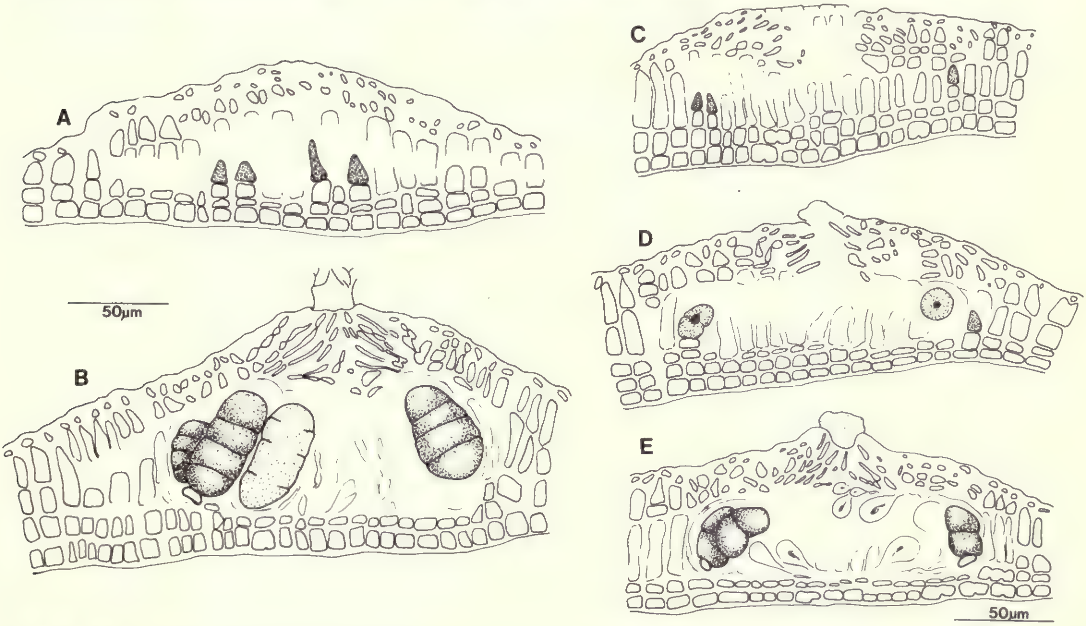

Fig. 60 Vertical sections of tetra/bisporangial conceptacles of *Pneophyllum concollum*. A, bisporangial initials (shaded). B, Mature bisporangial conceptacle. C, Tetrasporangial initials (shaded). D, Immature tetrasporangial conceptacle. E, Mature bisporangial conceptacle with distended columella and ostiole cells (arrow).

FORM RANGE: Plants collected in Ireland between April and August and subtidal material collected from the Scilly Isles and Lundy in July have noticeably thinner crusts with flatter conceptacles than material collected at Beer during winter. The thickness of the Beer crusts, and often heavy infestation of the conceptacles with bacteria and general detritus (Fig. 57A), suggest that the plants were growing under unfavourable conditions, while the thinner crusts from elsewhere were probably growing healthily and rapidly under favourable conditions.

DISTRIBUTION:
British Isles: Hampshire, Dorset, Devon, Cornwall, Jersey, Co. Wexford, Co. Clare, Co. Galway.
World: Northern France.

The frequency with which this species occurs in collections from Ireland suggests that it is one of the commonest simple crustose epiphytes there; it becomes much less common towards the eastern British Isles and has been collected, for example, only occasionally at Kimmeridge and Bembridge. Other than Le Jolis's samples on *Bornetia* collected from the Cherbourg area only one specimen has been collected from France (Y. M. Chamberlain, Gatteville, Normandy, 25 July 1977).

HABITAT: *Pneophyllum concollum* occurs as an epiphyte on the following algae: *Furcellaria lumbricalis, Calliblepharis ciliata, Gracilaria verrucosa* (Huds.) Papenf., *Chondrus crispus, Palmaria palmata, Bornetia secundiflora* (in France), *Gastroclonium ovatum* (Huds.) Papenf., *Laurencia pinnatifida, Polysiphonia elongata, Desmarestia aculeata* (L.) Lamouroux, *Laminaria hyperborea* (Gunnerus) Foslie, *L. ochroleuca* Bach. Pyl., *Cladostephus spongiosus* (Huds.) Agardh, *Cystoseira foeniculacea* (L.) Grev.; it was also found once growing on the leathery egg case of a nursling fish.

The species has been found intertidally in pools and areas of shore which do not dry out and subtidally to a depth of about 8 m. A population of *Pneophyllum concollum* growing together with *P. rosanoffii* on *Palmaria palmata* at Beer is discussed in Chamberlain (1982).

TAXONOMIC NOTE: It is possible *P. concollum* may belong to the same taxon as *P. myriocarpum* (*q.v.*).

Table 20 Dimensions of vegetative structures (in μm unless stated).

Pneophyllum concollum		British Isles
crust diameter		up to *c.* 5 mm
crust depth		up to *c.* 75
crust cell	length	(6·5) 12·5 (22·5)
surface	width	(4) 8·5 (15·5)
crust cell	height	*c.* 13
epithallial cell	length	(3) 4·5 (6·5)
surface view	width	(3) 5·5 (8)
epithallial cell	height	*c.* 5–7
hypothallial cell	width	(4·5) 11 (18)
VS	height	(5·5) 8·5 (16)
perithallial	width	(6·5) 10 (14·5)
cell	height	(4·5) 11·5 (28·5)
VS	number	up to 8
trichocyte type		—
trichocyte	length	
surface view	width	

RIDGWAY COLOUR CODE: dry crust – pale laelia pink

8. Pneophyllum myriocarpum (P. Crouan & H. Crouan) Y. Chamberlain, **comb. nov.**

BASIONYM: *Melobesia myriocarpa* P. Crouan & H. Crouan, *Florule du Finistère*: 150 (1867).

NOMENCLATURAL SYNONYM: *Melobesia myriocarpa* P. Crouan & H. Crouan in *Bull. Soc. bot. Fr.* **1860**: 4 (1860), nomen nudum; Foslie in *K. nor. Vidensk. Selsk. Skr.* **1899** (7): 10 (1900 ['1899']).

REFERENCES: *Melobesia* (subgenus *Pliostroma*) *zonalis* forma *myriocarpa*, Foslie; Foslie in *K. nor. Vidensk. Selsk. Skr.* **1908** (11): 4 (1908); Hamel and Lemoine in *Archs Mus. natn. Hist. nat. Paris* VII, **1**: 108 (1952 ['1953']).

Melobesia (subgenus *Pliostroma*) *zonalis* sensu Lemoine in *Bull. Lab. marit. Mus. Hist. nat. St. Servan* **7**: 20 (1931).

Table 21 Dimensions of reproductive structures (μm unless stated).

Pneophyllum concollum	British Isles
CARPOSPORANGIAL CONCEPTACLE	
external diameter	
surface diameter	(96) 159 (182)
VS internal diameter	(91) 136 (156)
VS height	(52) 65 (83)
VS roof height	(13) 20 (29)
roof type	uniform or irregular
no. basal cell rows	1–4
ostiole	collar-like (± spout)
no. gonimoblast filaments	up to *c.* 20
diameter carpospore	
SPERMATANGIAL CONCEPTACLE	
VS/surface width	(20) 47 (65)
VS height	19–37
length spermatium	3–5
width spermatium	1·5–2
TETRASPORANGIAL CONCEPTACLE	
external diameter	
surface diameter	(130) 148 (182)
VS internal diameter	(104) 151 (208)
VS height	(39) 75 (104)
VS roof height	(10) 21 (29)
roof type	uniform or irregular
no. basal cell rows	1–3
ostiole	collar-like (± spout)
no. tetrasporangia	*c.* 16–20
length tetrasporangium	(30) 47·5 (65)
width tetrasporangium	(19) 28·5 (41)
BISPORANGIAL CONCEPTACLE	
external diameter	
surface diameter	(104) 136 (182)
VS INTERNAL DIAMETER	(104) 135 (182)
VS height	(52) 91 (104)
VS roof height	(13) 29 (104)
roof type	uniform or irregular
no. basal cell rows	1–4
ostiole	collar-like (± spout)
no. bisporangia	*c.* 16–20
length bisporangium	(33·5) 45·5 (52)
width bisporangium	(15·5) 27·5 (42)

Melobesia zonalis sensu Batters pro parte in *J. Bot. Lond.* **40** (suppl.): 96 (1902).
Fosliella (subgenus *Heteroderma*) *zonalis* forma *myriocarpa* sensu Bressan in *Boll. Soc. adriat. Sci. nat.* **59**: 78 (1974).

SPECIMEN: *Melobesia zonalis* sensu Foslie (1900*a*). Coll. Brebner, Cawsand Bay, 11.11.1895, on rissoids (BM Algal Box Collection no. 506!) (Fig. 62E).

EXCLUDED RECORD: *Melobesia myriocarpa* sensu Holmes, *Alg. Br. rar.* 218. (= mixture of species but mainly *Pneophyllum confervicolum*) (BM!).

LECTOTYPE: CO! Herb. P.-L. and H.-M. Crouan, 12 December 1856, Rade de Brest (Figs 61A, B) Slide: Chamberlain no. 1391.

DIAGNOSIS: Epilithic species with thallus composed of hypothallium and epithallium only, ostiole forming a collar: differing from *P. plurivalidum, P. lobescens, P. zonale,* and *P. concollum* in having a vegetative thallus of hypothallium and epithallium only, and from *P. zonale* in not having long ostiolar filaments.

DESCRIPTION: Smooth, brownish-pink crusts composed of hypothallium and epithallium only, up to *c.* 50 mm diameter, *crust cells* in surface view robust, oblong, 11·5–15·5 μm long × 6–12 μm wide, *epithallial cells* 2·5–5·5 μm long × 4–9 μm wide, intrafilament and branch cell *trichocytes* of similar size to crust cells; conceptacles prominent, domed, crowded, all except spermatangial conceptacles with beaked collar-like ostioles, *carposporangial conceptacles* 83–130 μm internal diameter, 78–104 μm high, *spermatangial conceptacles* small, prominent or immersed beside carpogonial conceptacles, with ostiole prolonged into a spout, 27–55 μm wide × 39–47 μm high, *tetrasporangial conceptacles* 109–156 μm internal diameter × 96–143 μm high, up to 16 tetrasporangia per conceptacle, 44–64 μm long × 24–42 μm wide; *bisporangial conceptacle* (one only) 117 μm internal diameter × 91 μm high, bisporangium 48 μm long × 26 μm wide.

HISTORICAL: This taxon was first described by the Crouan brothers (1867, as *Melobesia*) on material dredged from the 'Rade de Brest, 12 Décèmbre 1856' (Figs 61A, B). Two sheets bearing this species are present in Herb. Crouan (CO); the samples comprise similar pieces of porcelain which bear crusts of *Pneophyllum* and are presumably part of the same collection. The sheet shown in Figures 61A, B has been selected for lectotype material, however, since the other

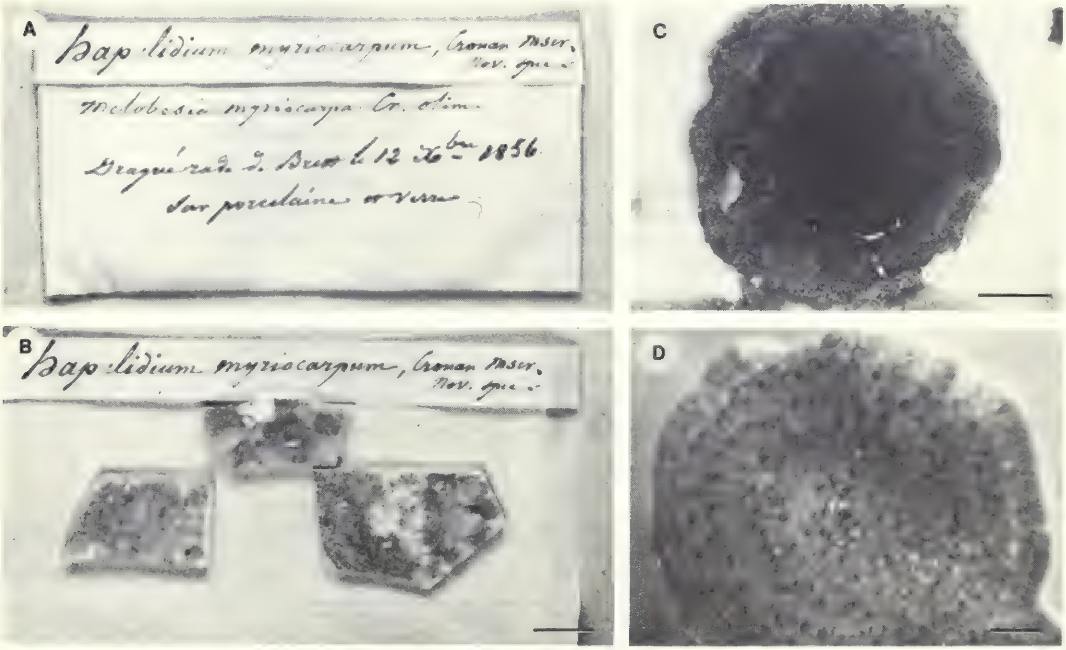
A
Hapalidium myriocarpum, Crouan mscr. nov. spec.
Melobesia myriocarpa Cr. olim.
Draguée rade de Brest le 12 Xbre 1856
sur porcelaine et verre
C
B
Hapalidium myriocarpum, Crouan mscr. nov. spec.
D

Fig. 61 Type specimen of *Pneophyllum myriocarpum* and appearance of cultured tetrasporangial crusts. A, Lectotype specimen of *Melobesia myriocarpa* P. Crouan & H. Crouan, Herb. Crouan, Concarneau. Packet closed. B, As A, packet open. Scale = 10 mm. C, Mature tetrasporangial crust with crust centre starting to become detached (seen in transmitted light). Scale = 5 mm. D, Young tetrasporangial crust (seen in reflected light). Scale = 1 mm.

sheet is one of the Crouans' decoratively mounted specimens lacking collection details. Crusts of more than one species are present on the lectotype sheet, but crusts of the present species predominate. The *P. myriocarpum* crusts have thin thalli with large crust cells and prominent conceptacles. A permanent slide (Chamberlain 1391) was made from a tetrasporangial crust. Annotations on the Crouans' specimen (Fig. 61A) show that they initially classified the present alga as a species of *Hapalidium* (i.e. with a single layer of thallus cells), but they eventually published it as *Melobesia* (i.e. with more than one layer of thallus cells) despite its thin thallus. The species was described (P.-L. & H.-M. Crouan, 1867) as having thin, pink discs which were often confluent, with lobed edges; the conceptacles were very small, hemispherical, very numerous and covering the entire crust; the spores were elliptic and transversely divided into four.

Two further Crouan specimens are present in Paris (PC); one, in the Herbier de France, is another piece of the same crust-bearing porcelain as that at Concarneau. The second specimen is in the *Melobesia myriocarpa* (*zonalis*) folder in Herb. Thuret and has been annotated by Thuret as follows: 'Cet échantillon, que j'ai reçu du frère des algologues brestois et qu'il a ainsi* nommé, "parce que la plante est vert jaune", ne paraît pas répondre a l'éspèce que MM Crouan ont désignée sous ce nom. Semble plutôt devoir être raprochée du *Melobesia myriocarpa*'. I did not examine either of these specimens microscopically because they are very sparse and firmly attached to the substrate, but presumably one or both of them were sent to Foslie when he was preparing his analysis of Crouan species (Foslie, 1900*a*). In this publication Foslie concluded that *M. myriocarpa* was conspecific with *M. zonalis*. Later Foslie (1908*a*) gave it the status of *M. zonalis* f. *myriocarpa* and then commented (Foslie, 1908*b*) 'it corresponds to *M. farinosa* f. *solmsiana* and *M. minutula* f. *lacunosa* with a very irregular, often subdichotomous thallus'. Foslie (1909) transferred *M. zonalis* to *Heteroderma* subgenus *Pliostroma* but did not list forma *myriocarpa* in this publication.

Holmes (Alg. Br. rar. 218) identified crutose coralline epiphytes on *Laminaria* blades (BM: Ferry Bridge (Weymouth), August 1893 and Weymouth, August 1895) as *Melobesia myriocarpa* (listed as *M. zonalis* in Batters (1902)). Foslie (1905*a*) reidentified these crusts as a mixture of *Fosliella farinosa* (as *Melobesia*) and *Pneophyllum limitatum* (as *Melobesia lejolisii*†). I examined some of these specimens (BM) and found mainly *Fosliella farinosa* and *Pneophyllum confervicolum* with some *P. limitatum*. A further collection included in Batters' (1902) records of *Melobesia zonalis* is from Cawsand Bay, Plymouth (BM Algal Box Collection no. 506, coll. Brebner, 11.11.1895) and comprises numerous crust-covered rissoid shells (Fig. 62E). The crusts were initially named *Melobesia lejolisii* on the specimens, but were reidentified by Foslie (1900*a*) as *M. zonalis*. I have examined these crusts and find them to be mainly *Pneophyllum myriocarpum*.

In common with epilithic species of *Pneophyllum* generally, no description of *P. myriocarpum* has been published since Foslie's work. It has been recorded only rarely and seems to have been regarded as a form of *P. zonale* characterised by having crusts smothered with small, hemispherical conceptacles (e.g. Hamel & Lemoine, 1953, as *Melobesia zonalis* f. *myriocarpa*; Bressan, 1974, as *Fosliella zonalis* f. *myriocarpa*). I have not examined the samples on which any of these records were based.

The written description of *Fosliella tenuis* (Adey & Adey, 1973, p. 398) as having extremely thin, nearly transparent crusts composed of hypothallium and epithallium only, possibly refers to the present species, although the illustrative diagrams (Adey & Adey, 1973, Tab. XIV) refer to their slide of the type which is material of *Pneophyllum zonale* (Fig. 82E). The rock specimen (BM, Algal Box Collection no. 1171) which bears crusts identified as *Fosliella tenuis* by W. H. Adey bears some crusts of the present species.

CRUST APPEARANCE: In laboratory culture (Chamberlain, 1982) *P. myriocarpum* forms thin (up to *c.* 25 μm deep), translucent, brownish-pink, epilithic crusts (Figs 61C, D) which are strongly adherent. The crust edge may produce fan-like outgrowths under unfavourable conditions and the crusts may grow up to about 30 mm diameter before the central part loosens and becomes detached (Fig. 61C).

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* presumably it was sent as *M. zonalis* by the Crouans' brother.

† accepting Rosenvinge's (1917) statement that Foslie came to regard all *M. lejolisii* growing on algae as forma *limitata*.

Under the S.E.M. (Fig. 62F) the crust cells are regularly rectangular, with epithallial concavities about twice as wide as long. Intrafilament (and very occasionally branch cell) trichocytes occur; they are the same size as normal crust cells, and an epithallial concavity is

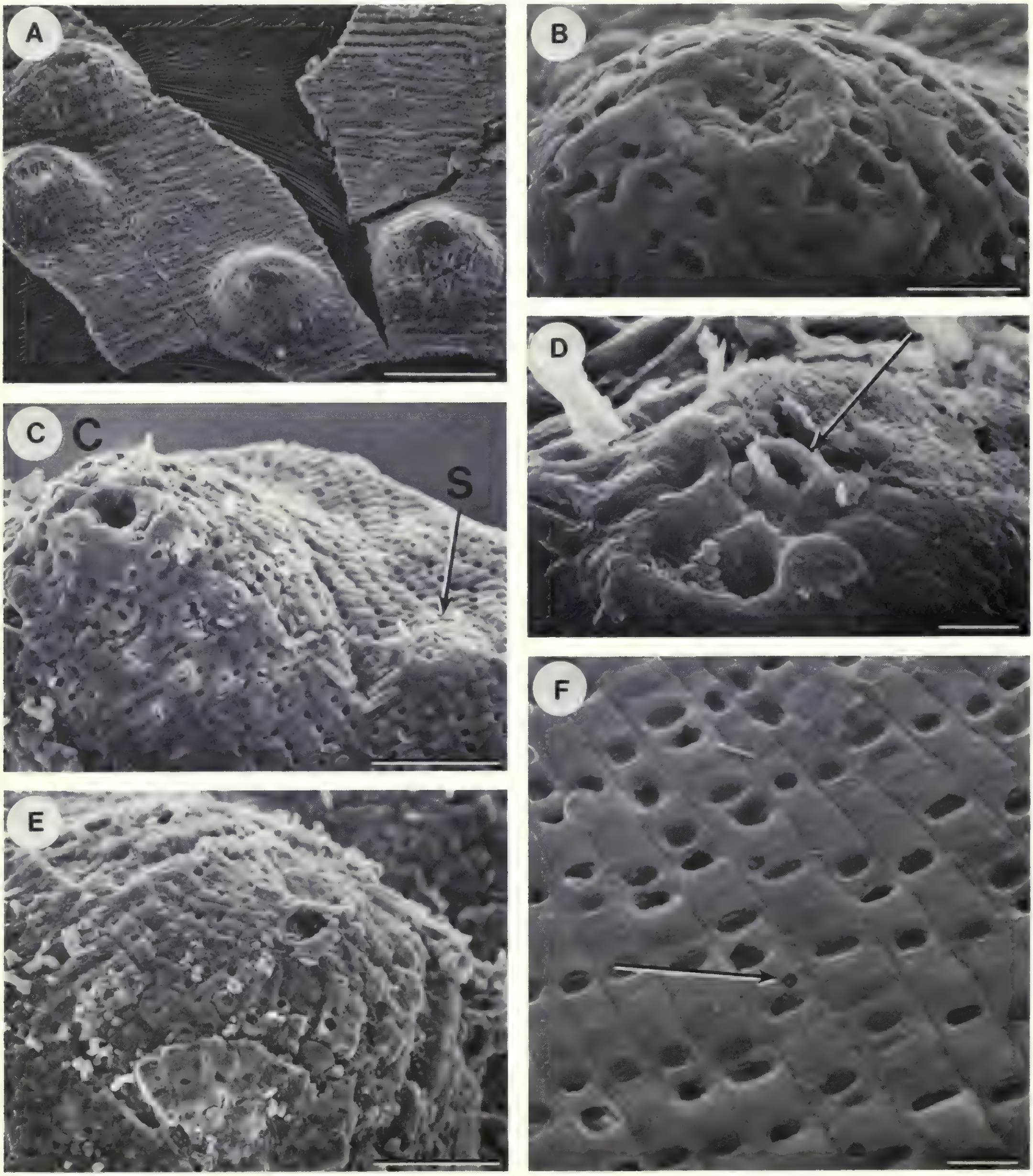

Fig. 62 Scanning electron micrographs of *Pneophyllum myriocarpum*. A, Tetrasporangial crust (critical point dried). Scale = 250 μm. B, Ostiole of tetrasporangial conceptacle. Scale = 25 μm. C, Gametangial crust showing carposporangial (c) and spermatangial (s) ostioles. Scale = 50 μm. D, Spermatangial ostiole with remains of spout (arrow). Scale = 5 μm. E, Conceptacle of crust growing on *Rissoa* sp. (coll. Brebner). Scale = 50 μm. F, Crust cells with trichocytes (arrow). Scale = 10 μm.

usually present. The lower surface shows tube-like hypothallial filaments at the periphery, and a flattened surface towards the centre.

The conceptacles are abruptly prominent (Figs 62A, C, E), conical, or domed, and they often become extremely crowded. The conceptacle roof (Figs 62B, C, E) shows a jumble of filaments running at various levels and in different directions, which may also slough off. The ostiole is composed of filaments united into a small collar (Figs 62B, C, E).

When growing on rissoid shells on the shore (Fig. 62E) the thallus curves round the shell and the conceptacles are particularly crowded.

VEGETATIVE ANATOMY: *P. myriocarpum* is characterised by the thin, translucent crusts which are composed of robust, brick-shaped cells (Figs 63A, B) which in living material are brownish-pink in transmitted light; in cultured crusts the cells are full of floridean starch grains. Branch cell, and rarely intrafilament, trichocytes (Fig. 63B) are common under warm, long daylength conditions, and are of similar size to the crust cells. Large, abnormal, terminal trichocytes occur occasionally (Chamberlain, 1982); they appear to be similar to those recorded for *P. limitatum* by Suneson (1943, as *Melobesia*).

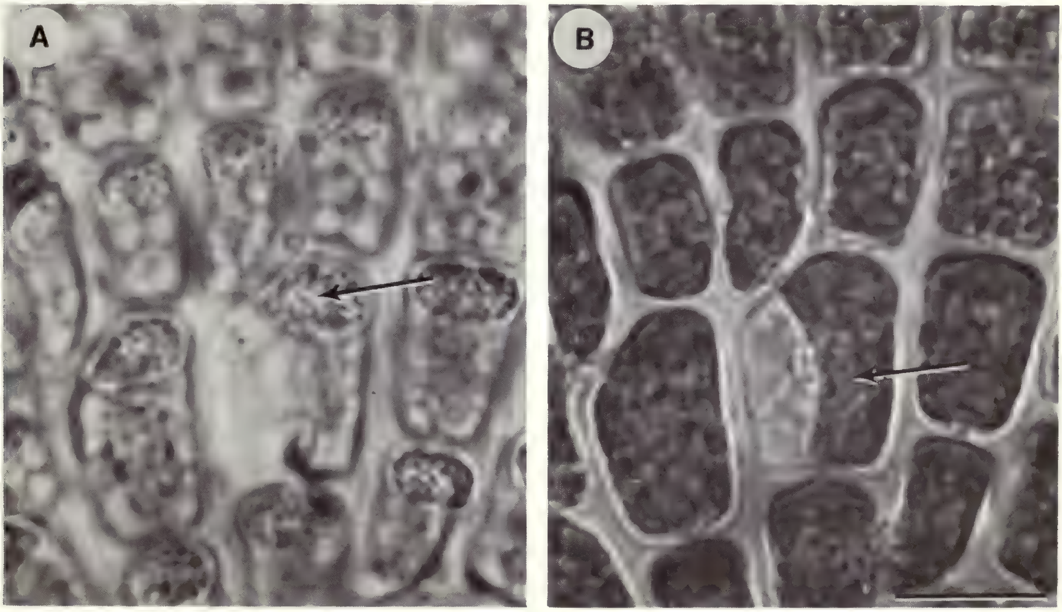

Fig. 63 Crust cells of *Pneophyllum myriocarpum*. A, Focused to show epithallial cells (arrow). B, Focused to show hypothallial cells and trichocyte (arrow). Scale = 10 μm.

GAMETANGIAL PLANTS: The crusts are monoecious with spermatangial conceptacles closely adjacent to carpogonial conceptacles (Figs 62C, D; 65E); they can clearly be seen in surface view on crusts growing on glass (Fig. 64F). The spermatangial conceptacles may be immersed in the edge of the carpogonial conceptacles (Fig. 64A) or prominent and dome-shaped (Fig. 65E). Elongated spermatangia are cut off at two sites on each initial (Fig. 65E) and when released the spermatangia are oval. The ostiole is prolonged into a spout which is occasionally forked.

The carpogonial conceptacles (Fig. 64A) are raised and develop by the growth, stretching and rupture of perithallial cells; the centrally-borne procarps bear one or two carpogonia (Fig. 65A). As the conceptacle grows, filaments develop round the ostiole (Fig. 65A), and substantial downward-growing filaments are evident in many carpogonial conceptacles. Although the conceptacles rise abruptly from the thin thallus, a considerable amount of perithallial development contributes to the structure of the conceptacle wall.

CARPOSPORANGIAL CONCEPTACLES: In carposporangial conceptacles the downward ostiolar filaments (Figs 64D, E; 65D) are well-developed, while the upper ones fuse and extend into an hyaline collar (Figs 64D, E; 65C, D). The fusion cell is usually rather flat. A fusion cell (Fig. 65B) was extruded from a conceptacle and the cell is seen to be somewhat segmented; there are the remnants of a number of procarps on the upper surface and the carposporangial filaments are initiated peripherally.

TETRASPORANGIAL PLANTS: Tetrasporangial plants bear crowded conceptacles (Fig. 62A) which are similar to carposporangial conceptacles in structure and development, but usually somewhat larger. The tetraspores are borne peripherally and there is often considerable development of columella-like, central sterile paraphyses (Figs 64C; 66B). Young tetrasporangia are shown in Figure 66A. Tetrasporangia are very crowded in mature conceptacles and up to about 16 occur per conceptacle.

BISPORANGIAL PLANTS: Only one bisporangial plant was found in British Isles collections of *P. myriocarpum* and this was seen only as a single section made on shore-collected material. Bisporangial conceptacles are common, however, among the crusts collected from the aquarium glass at Roscoff, and it can be seen (Fig. 64B) that the conceptacles are similar to tetrasporangial conceptacles. Bisporangia are more numerous than tetrasporangia, however, with up to about 40 being found in a single conceptacle.

PHENOLOGY: Very little is known about the periodicity of *P. myriocarpum* on the shore although all the verified collections (Crouan – December; Brebner – November; Yealm – October; Kimmeridge – throughout the summer; Roscoff aquarium – June; Co. Clare – June) are fertile. Tetrasporangial and gametangial crusts of *P. myriocarpum* have, however, been grown through several generations in laboratory culture (Chamberlain, 1982) under normal, seasonal day-length/temperature conditions and it has been found that, while it grows and reproduces at all seasons, growth and maturation are quicker during summer (April–October) than during the rest of the year.

At Kimmeridge, *P. myriocarpum* grows on rissoid shells; studies by Wigham (1975) show that only a few individuals in such rissoid populations survive the winter so that *P. myriocarpum* crusts must, therefore, mainly grow and reproduce during the summer.

FORM RANGE: The dimensions of British Isles and Roscoff samples of *P. myriocarpum* (Tabs 22; 23) suggest that there are no noticeable variations between the populations at these two localities. When grown in culture (Chamberlain, 1982) it was found that crust cells tended to be smaller in winter than summer and also that under very cold conditions areas of gametangial crust bearing only spermatangial conceptacles developed; adjacent carposporangial conceptacles were, however, initiated as conditions became warmer. In laboratory culture trichocytes were produced in summer but not in the winter months (Chamberlain, 1982).

DISTRIBUTION:

British Isles: Kent, Dorset, Devon, Co. Clare.

World: France, Italy.

It is probable that *P. myriocarpum* occurs widely at least in Europe, but very little is known at present about epilithic simple, crustose Corallinaceae.

HABITAT: *P. myriocarpum* is known to grow on fragments of glass and china and on shells, typically rissoids; it probably also grows on rocks. As an epilith, *P. myriocarpum* probably grows mainly in subtidal areas where it is not in danger of drying out since laboratory culture experiments have shown that it is unable to tolerate more than a very few minutes of desiccation. When growing on shells, however, *P. myriocarpum* is found in the intertidal zone. The only population which has been studied of this type is at Kimmeridge (Fig. 18). At this locality, *Halopitys incurvus* is a common intertidal alga growing in shallow pools on the ledges; during the summer this alga houses large populations of rissoids many of which are covered with crusts of *P. myriocarpum*. Although many plants of *Halopitys* dry out considerably during hot weather since

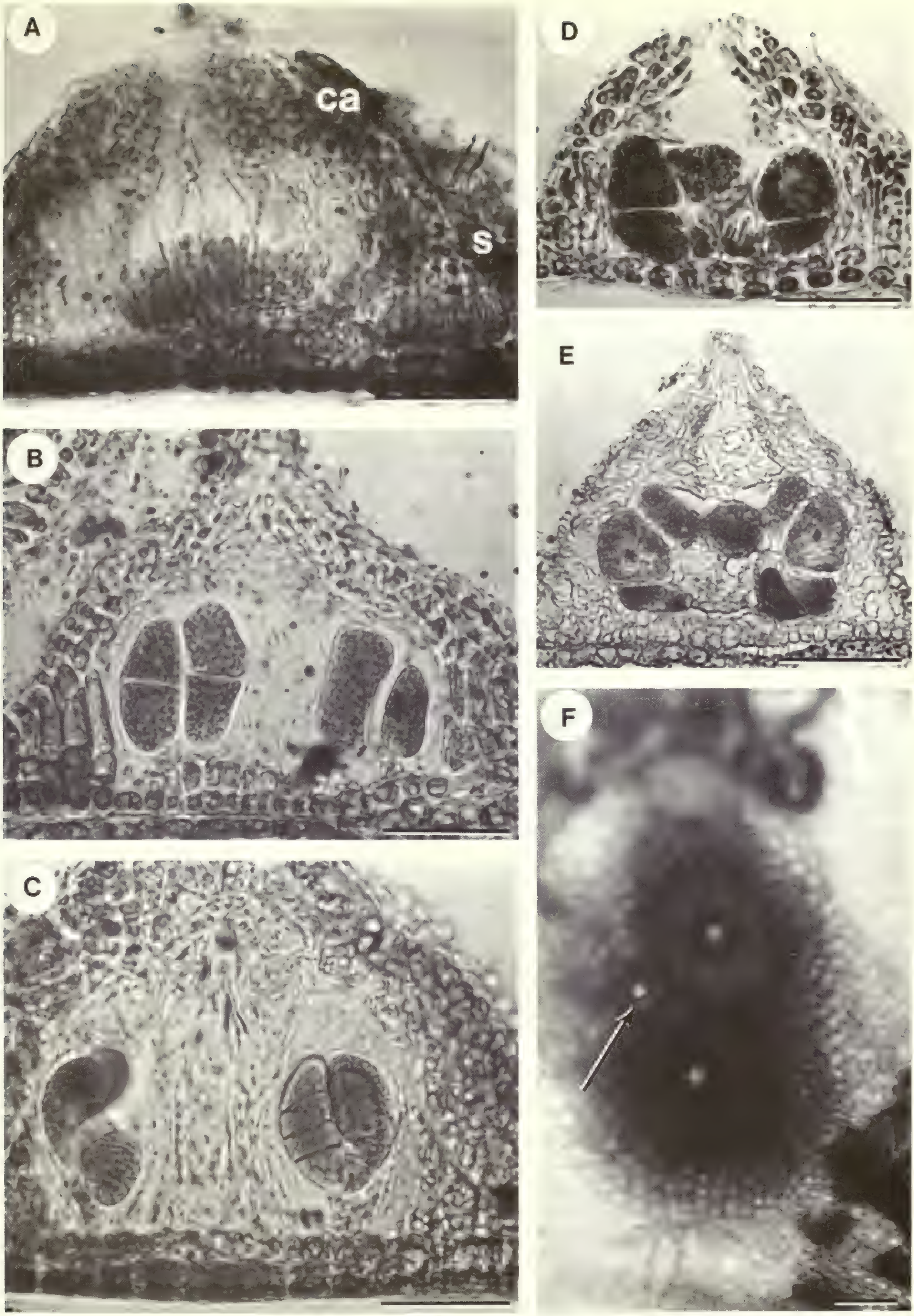

Fig. 64 Reproductive features of *Pneophyllum myriocarpum*. A, Vertical section of gametangial crust with carpogonial (ca) and spermatangial (s) conceptacles. Scale = 50 μm. B, Vertical section of bisporangial conceptacle. Scale = 50 μm. C, Vertical section of tetrasporangial conceptacle. Scale = 50 μm. D, Vertical section of carposporangial conceptacle with simple ostiole. Scale = 50 μm. E, Vertical section of carposporangial conceptacle with ostiolar spout. Scale = 50 μm. F, Surface view of growing crust with two carposporangial and one spermatangial (arrow) conceptacles. Scale = 100 μm.

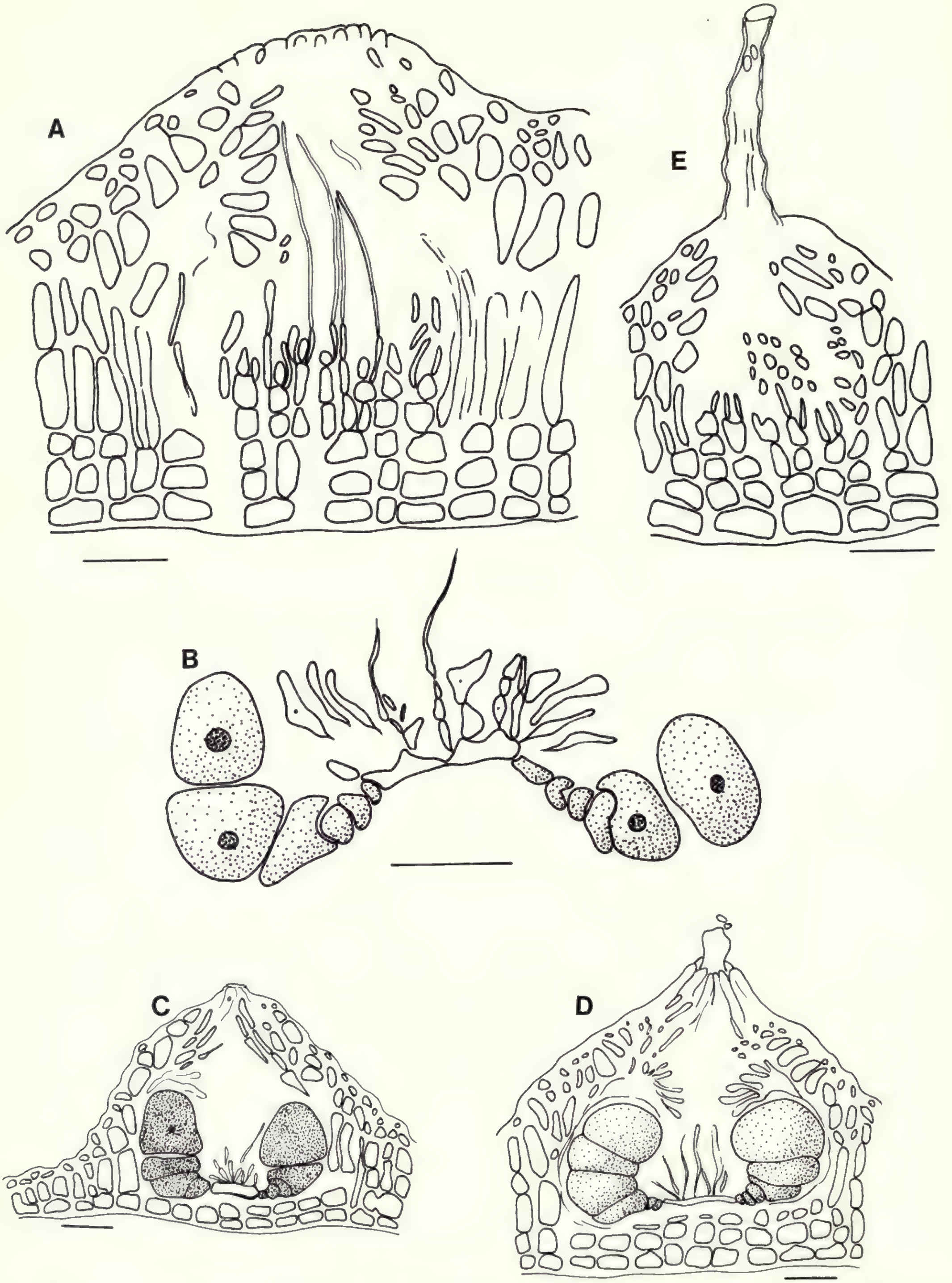

Fig. 65 Gametangial and carposporangial structures of *Pneophyllum myriocarpum*. A, Vertical section of carpogonial conceptacle. B, Fusion cell and two carposporangial filaments extruded from conceptacle. C, & D, Vertical section of two carposporangial conceptacles to illustrate differences in size and degree of immersion. E, Vertical section of spermatangial conceptacle. Scale = 20 μm (all figures).

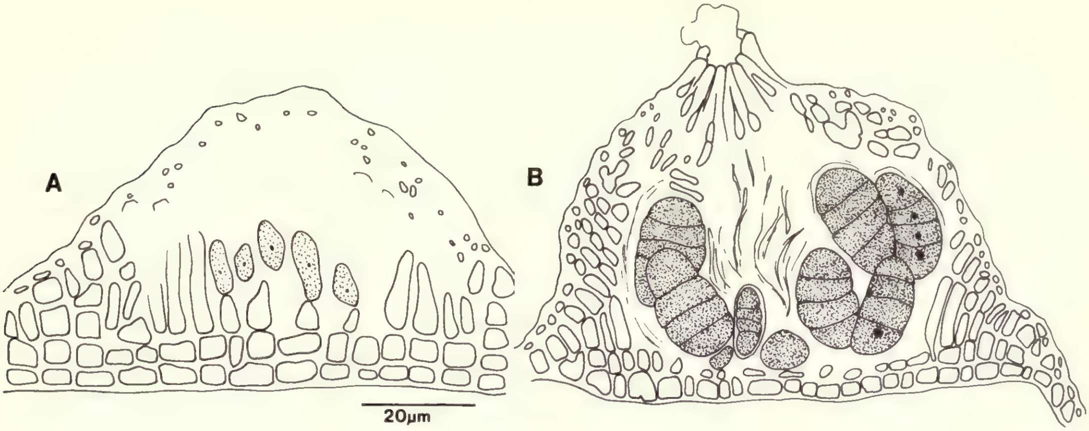

Fig. 66 Vertical sections of tetrasporangial conceptacles of *Pneophyllum myriocarpum*. A, Tetrasporangial initials (shaded). B, Mature conceptacle.

they are in shallow pools, the rissoids move into the central parts of the plant which usually remain moist, and their attendant *Pneophyllum* crusts are saved from desiccation in this way.

LIFE HISTORY: A regular alternation of gametangial/carposporangial and tetrasporangial phases has been found in this species growing in laboratory culture (Chamberlain, 1982).

TAXONOMIC NOTE: *Pneophyllum myriocarpum* and *P. concollum* appear very distinct when at their most characteristic. The epiphytic crusts of *P. concollum* have a well-developed perithallium and broad, slightly raised conceptacles, while epilithic crusts of *P. myriocarpum* lack a perithallium and have abruptly conical conceptacles. However, the collar-like ostiole is essentially similar in both species; in addition, crusts of *P. concollum* may have only a slightly developed perithallium, while Irish samples of *P. myriocarpum* growing on shells have deeper crusts than usual. It is possible, therefore, that further research may indicate that both species must be referred to the same taxon: if so, *P. concollum* will have to be subsumed in *P. myriocarpum*.

9. **Pneophyllum lobescens** Y. Chamberlain, **sp. nov.**

REFERENCE: *Melobesia zonalis* sensu Batters pro parte in *J. Bot., Lond.* **40** (Suppl.): 96 (1902) (this refers to the specimens below).

SPECIMENS: *Melobesia myriocarpa* sensu Batters, Duke's Rock, Plymouth, 7 April, 1897 and Plymouth 12 March, 1900 (both in BM Algal Box Collection no. 505!).

HOLOTYPE: BM! Y. M. Chamberlain no. 77/228, 29 October 1977, mouth of River Yealm, south Devon, at a depth of 8 m. Culture material nos. 104/4/5a gametangial, 104/27 tetrasporangial and 104/4/3/b bisporangial.

DIAGNOSIS: Species epilithica cellulis crustae latioribus, filamentis perithallii profunditate usque ad 6 cellulas et ostiolis tholiformibus: a *P. plurivalidio* differt trichocytis non modo intra filamenta sed etiam ramos facientibus et absentia cellularum crustae longarum et sinu osarum, a *P. zonali* absentia filamentorum ostiolarium longorum, et a *P. myriocarpio* perithallio profundo differt.

DESCRIPTIO: Crustae phloginae ad ferruginescentes, diametro usque ad 10 mm, profunditate 90 μm, margine regulari, sed saepe lobescenti quum condiciones infavorabiles sunt, perithallium media in crusta profunditate usque ad 6 cellulas, *cellulae perithallii* (in sectione verticali) 8–16 μm latae × 8·5–23 μm altae, margo crustae ex hypothallio et epithallio modo constatus, *cellulae crustae* aspectu superficiali relative latae, 6·5–16·5 μm longae × 4·5–11 μm latae, *cellulae epithallii* 3–4·5 μm longae × 4·5–11 μm latae, *trichocyti* et intra filamenta et ramos facientes frequentes, amplitudine eadem ac cellularum crustae; conceptacula immersa, velut circuli indefiniti pallidi in crusta magis atrata, omnia, praeter ea spermatan-

Table 22 Dimensions of vegetative structures (in μm unless stated).

Pneophyllum myriocarpum	British Isles	Roscoff aquarium	Crouan type specimen
crust diameter	30–50 mm		
crust depth	*c.* 50		
crust cell length	(11·5) 14·5 (15·5)	(10) 13 (14·5)	(10·5) 13 (15)
surface width	(6) 10·5 (12)	(6·5) 9·5 (12)	(6·5) 8 (10)
crust cell height	*c.* 13		
epithallial cell length	(2·5) 4 (5·5)	(3) 3·5 (4·5)	(4) 4·5 (5)
surface view width	(4) 6·5 (9)	(5·5) 7·5 (9·5)	(5) 6 (7)
epithallial cell height	3–4		
hypothallial cell width			
VS height			
perithallial width			
cell height			
VS number			
trichocyte type	intrafilament (occasionally branch cell)	one branch cell type seen	
trichocyte length	as crust cells		
surface view width	as crust cells		

RIDGWAY COLOUR CODE: dry crust – dull indian purple, pl. XLIV
fresh crust – dark vinaceous, pl. XXVII

gialia, tholo ostioli in superficiei superiore, *conceptacula carposporangialia* diametro interno 88–112 μm, altitudine 46–68 μm; *conceptacula spermatangialia* immersa, 34–52 μm lata, 35–48 μm alta, ostiolo in canalem producto, *conceptacula tetrasporangialia* diametro interno 104–138 μm, altitudine 65–91 μm, usque ad 18 tetrasporangiis peripheralibus in unoquoque conceptaculo, paraphysibus centralibus sterilibus instructa, tetrasporangia 43–54·5 μm longa × 24·5–41·5 μm lata, *conceptacula bisporangialia* diametro interno 82–134 μm, altitudine 59–93 μm, usque ad 20 bisporangiis peripheralibus in unoquoque conceptaculo, paraphysibus centralibus sterilibus instructa, bisporangia 36·5–51 μm longa × 19·5–35 μm lata.

DIAGNOSIS: Epilithic species with rather broad crust cells, perithallial filaments up to 6 cells deep and domed ostiole: differing from *P. plurivalidum* in having branch cell as well as intrafilament trichocytes and in lacking long, sinuous crust cells, from *P. zonale* in not having long ostiolar filaments and from *P. myriocarpum* in having a deep perithallium.

DESCRIPTION: Crusts bright pink to brownish-pink, up to *c.* 10 mm diameter, 90 μm deep, margin regular or often becoming lobed under unfavourable conditions, perithallium up to 6 cells deep in crust centre, *perithallial cells* (in VS) 8–16 μm wide × 8·5–23 μm high; crust border of hypothallium and epithallium only, *crust cells* in surface view relatively broad, 6·5–16·5 μm long × 4·5–11 μm wide, *epithallial cells* 3–4·5 μm long × 4·5–11 μm wide, intrafilament and branch cell *trichocytes* common, of similar size to crust cells; conceptacles immersed, appearing as pale indefinite circles in darker crust, all except spermatangial conceptacles with ostiole dome, *carposporangial conceptacles* 88–112 μm internal diameter × 46–68 μm high, *spermatangial conceptacles* 34–52 μm wide × 35–48 μm high, with ostiole prolonged into a spout, *tetrasporangial conceptacles* 104–138 μm internal diameter × 65–91 μm high, up to 18 peripheral tetrasporangia per conceptacle, 43–54·5 μm long × 24·5–41·5 μm wide, central sterile paraphyses present, *bisporangial conceptacles* 82–134 μm internal diameter × 59–93 μm high, up to 20 peripheral bisporangia per conceptacle, 36·5–51 μm long × 19·5–35 μm wide, central sterile paraphyses present.

HISTORICAL: *P. lobescens* is a newly described, epilithic species of *Pneophyllum*. It was originally collected from the mouth of the River Yealm, south Devon, where it was growing, together with *P. zonale*, *P. plurivalidum*, and *P. myriocarpum*, on glass bottles at a depth of about 8 m and it

Table 23 Dimensions of reproductive structures (μm unless stated).

Pneophyllum myriocarpum	British Isles	Roscoff aquarium
CARPOSPORANGIAL CONCEPTACLE		
external diameter		
surface diameter	(70) 114 (156)	(117) 128 (143)
VS internal diameter	(83) 101 (130)	(99) 117 (130)
VS height	(78) 97 (104)	(50) 87 (117)
VS roof height	(13) 15 (31)	13–15·6
roof type	irregular	
no. basal cell rows	1 (rarely 2)	1
ostiole	beaked	beaked
no. gonimoblast filaments	*c.* 12	
diameter carpospore		
SPERMATANGIAL CONCEPTACLE		
VS/surface width	(27) 49 (55)	(27) 36 (42)
VS height	(39) 42 (47)	22–29
length spermatium		
width spermatium		
TETRASPORANGIAL CONCEPTACLE		
external diameter		
surface diameter	(106) 146 (171)	(120) 143 (156)
VS internal diameter	(109) 131 (156)	(143) 150 (156)
VS height	(96) 118 (143)	(117) 139 (161)
VS roof height	(13) 18 (26)	*c.* 13
roof type	irregular	
no. basal cell rows	1–2	1
ostiole	beaked	beaked
no. tetrasporangia	8–16	8–14
length tetrasporangium	(44) 53 (64)	(57) 58 (63)
width tetrasporangium	(24) 29 (42)	(31) 35 (42)
BISPORANGIAL CONCEPTACLE	one only	
external diameter		
surface diameter		(101) 111 (156)
VS internal diameter	117	(107) 122 (130)
VS height	91	(65) 97 (117)
VS roof height	21	(13) 15 (18)
roof type		
no. basal cell rows	2	1 (rarely 2)
ostiole	beaked	beaked
no. bisporangia		*c.* 20–*c.* 40
length bisporangium	48	(39) 44 (52)
width bisporangium	26	(17) 23 (29)

was subsequently grown in laboratory culture (Chamberlain, 1982). Two collections of Batters's (BM) were found to be of the same taxon; these were growing on razor shells at Plymouth on 12 March 1900 and on glass at Duke's Rock, Plymouth from a depth of 3–6 fathoms on 7 April 1897: Batters labelled them both '*Melobesia myriocarpa* Crouan' but he later listed them (Batters, 1902) as '*M. zonalis* Fosl.'.

Crust appearance: In laboratory culture (Figs 67A, B; 69A) *P. lobescens* forms rather thin (up to 90 μm deep), brownish or bright rosy-pink, epilithic crusts with pale edges which rapidly become irregularly lobed under unfavourable conditions. The crusts tend to detach easily and rarely grow to more than 10 mm diameter before the central part detaches.

Under the S.E.M. (Fig. 67G) the crust cells can be seen to vary from elongated to broad, and the epithallial concavities vary from rounded to about twice as wide as long; branch cell and

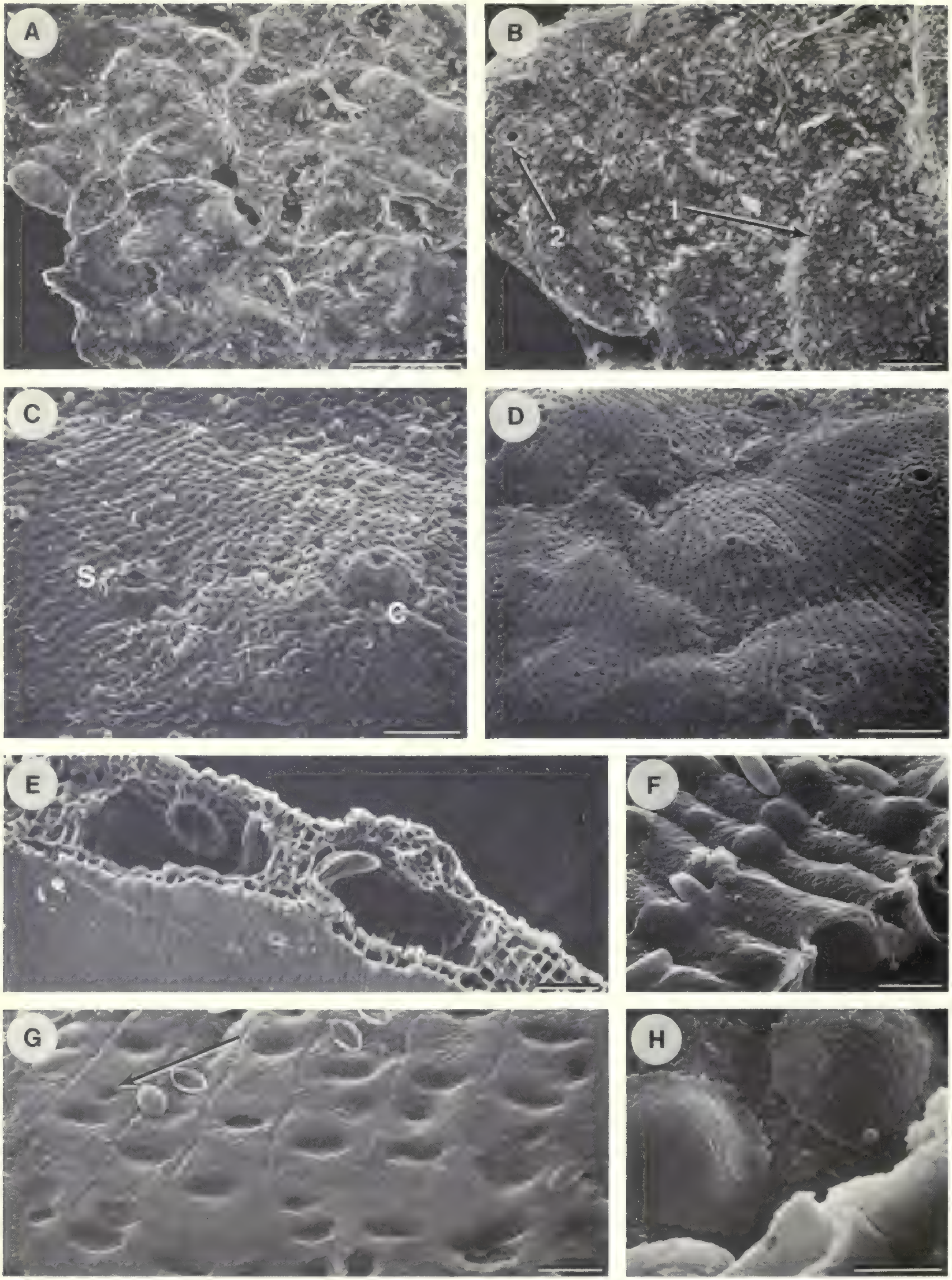

Fig. 67 Scanning electron micrographs of *Pneophyllum lobescens*. A, General view of crust. Scale = 500 μm. B, Enlarged view of A showing crust lobes (1) and ostioles (2). Scale = 100 μm. C, Gametangial crust showing carposporangial (c) and spermatangial (s) ostioles. Scale = 50 μm. D, Bisporangial crust. Scale = 100 μm. E, Vertical fracture through tetrasporangial conceptacles. Scale = 50 μm. F, Lower crust surface. Scale = 10 μm. G, Crust cells and trichocyte (arrow). Scale = 10 μm. H, Nodules from lower surface of crust. Scale = 5 μm.

intrafilament trichocytes occur. On the younger parts of the lower surface (Fig. 67F) the hypothallial filaments are tube-like, and calcareous nodules are frequent (Fig. 67H).

The conceptacles are immersed in the thallus (Figs 67C, D, E; 68A), and appear flat in fresh material; in dried material they are gently rounded, and appear as rather diffuse pale areas in a darker crust. The conceptacle roof is uniform and the ostiole is dome-like (Figs 68B, C, E).

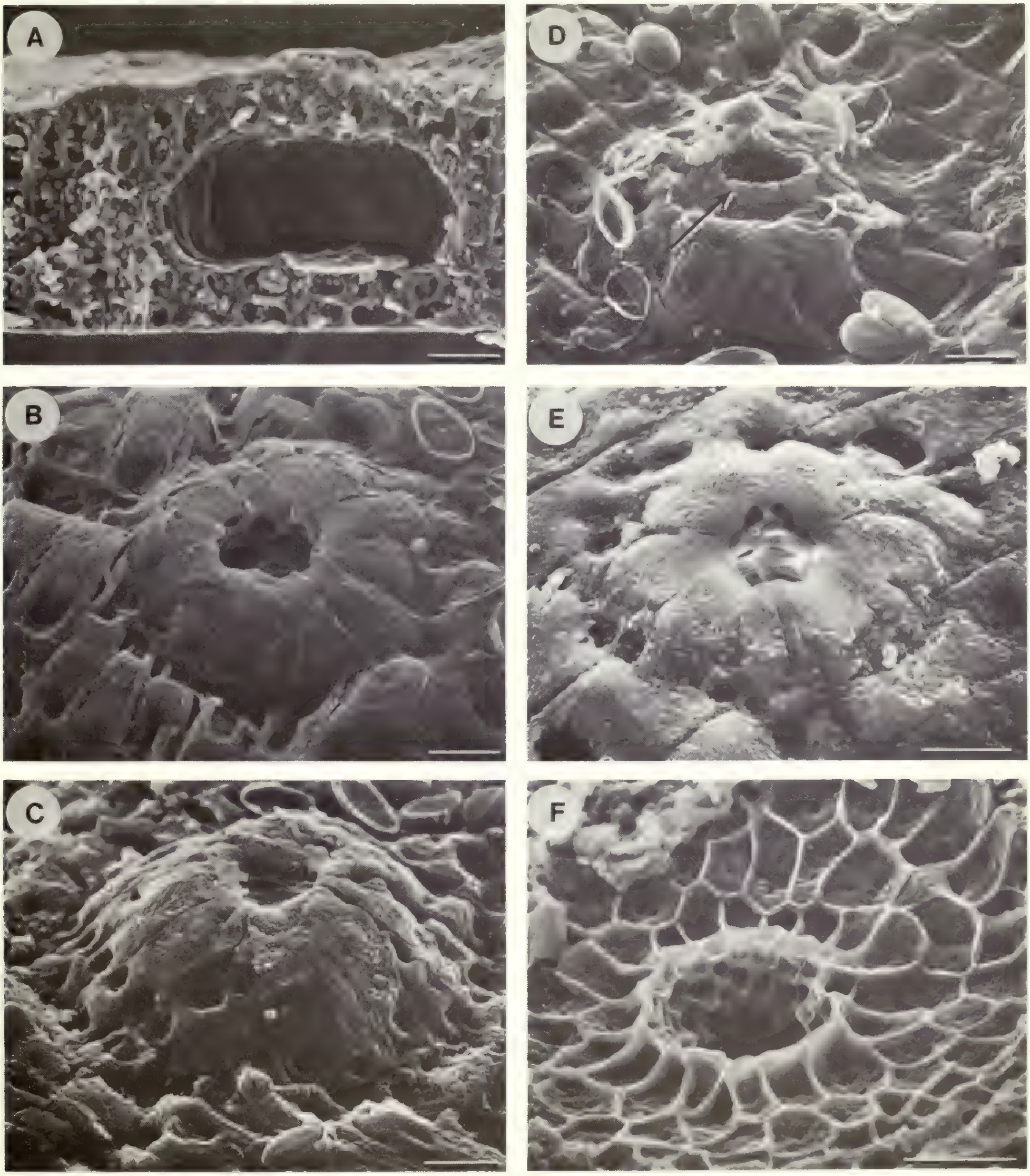

Fig. 68 Scanning electron micrographs to show conceptacle and ostiole features of *Pneophyllum lobescens*. A, Vertical section of carposporangial conceptacle. Scale = 25 μm. B, Young tetrasporangial ostiole. Scale = 10 μm. C, Mature carposporangial ostiole. Scale = 10 μm. D, Spermatangial ostiole with ruptured spout (arrow). Scale = 10 μm. E, Bisporangial ostiole. Scale = 10 μm. F, Underside of tetrasporangial conceptacle roof. Scale = 25 μm.

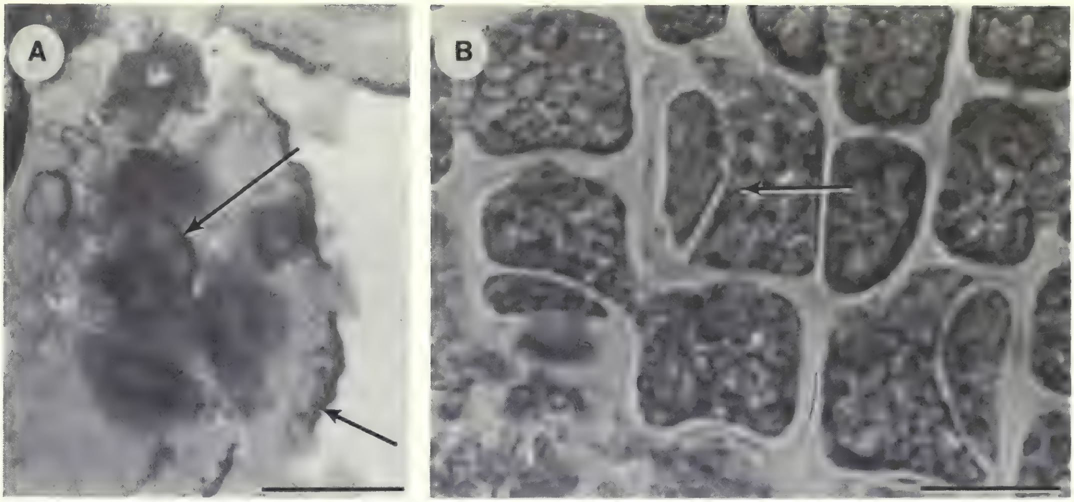

Fig. 69 Crust features of *Pneophyllum lobescens*. A, Bisporangial crust in culture showing thallus lobes (arrow). Scale = 50 μm. B, Bisporangial crust cells with trichocytes (arrow). Scale = 10 μm.

VEGETATIVE ANATOMY: The crust border is composed of hypothallium and epithallium only. In surface view (Fig. 69B) the crust cells vary from isodiametric to about one and a half times as long as wide, and usually contain many floridean starch grains. Epithallial cells vary from rounded rectangular to short and broad; they are dome-shaped to flattened in vertical section. Intrafilament and branch cell (Fig. 69B) trichocytes are common; they are about the same length as crust cells but often bulge sideways squashing adjacent cells.

In vertical section (Figs 70E; 72B) the thallus appears regularly zoned horizontally. The perithallial filaments vary from 1–6 cells deep and their cells vary from short to markedly elongated; these cells are full of starch grains.

GAMETANGIAL PLANTS: Gametangial plants are monoecious. The spermatangial conceptacles are adjacent to the carpogonial conceptacles (Figs 67C; 71A), and are flask-like chambers with a conspicuous ostiole and spout (Fig. 68D). The oval spermatia (Figs 70A; 71B) are larger (up to 8 μm long) than in most of the described species of *Pneophyllum*.

Carpogonial conceptacles (Fig. 71C) are immersed with one to two cell rows below the conceptacle. The procarps are often borne rather high in the conceptacle chamber, with conspicuous supporting cells and the central procarps bear one or two carpogonia with long trichogynes.

CARPOSPORANGIAL CONCEPTACLES: The mature conceptacle (Figs 67C; 68A; 70B; 71A, D) is immersed in the thallus with only the dome-like structure, formed from the upper ostiolar filaments, protruding above the thallus surface (Fig. 68C). The downward ostiolar filaments are well-developed (Fig. 71D), and the development pattern formed by the remnants of the perithallial cells and the roof and ostiole filaments to which they give rise is often particularly clear in this species. The fusion cell is quite deep (Fig. 71D), and the peripheral gonimoblast filaments are about five cells long with the carposporangium considerably larger than the penultimate cell (Figs 70B; 71D).

TETRASPORANGIAL PLANTS: Conceptacle shape and ostiole structure (Figs 67E; 68B, F; 70E; 72B) are similar to that seen in the carposporangial conceptacle. Young tetrasporangia (Fig. 72A) are interspersed with sterile cells, but mature tetrasporangia are borne peripherally (Figs 70E; 72B), and are plump and well-pigmented. A central columella of sterile cells is present, but the mature conceptacle is so full of tetrasporangia that the columella and the cells beneath the conceptacle are often squashed flat.

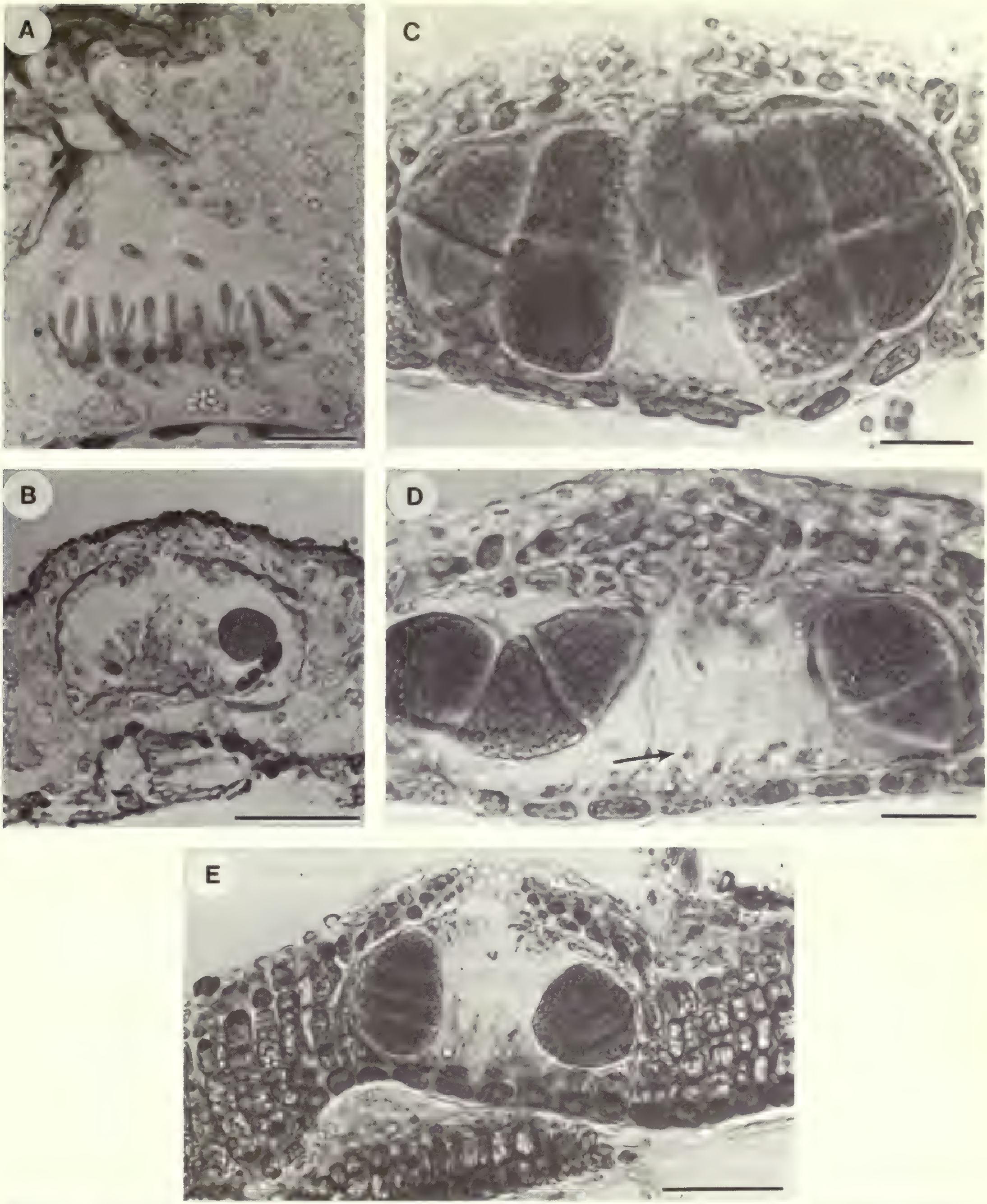

Fig. 70 Vertical sections of conceptacles of *Pneophyllum lobescens*. A, Spermatangial conceptacle. Scale = 20 μm. B, Carposporangial conceptacle. Scale = 50 μm. C, Bisporangial conceptacle showing crowding of mature bisporangia. Scale = 20 μm. D, Bisporangial conceptacle showing central sterile cells (arrow). Scale = 20 μm. E. Tetrasporangial conceptacle in a superimposed crust. Scale = 50 μm.

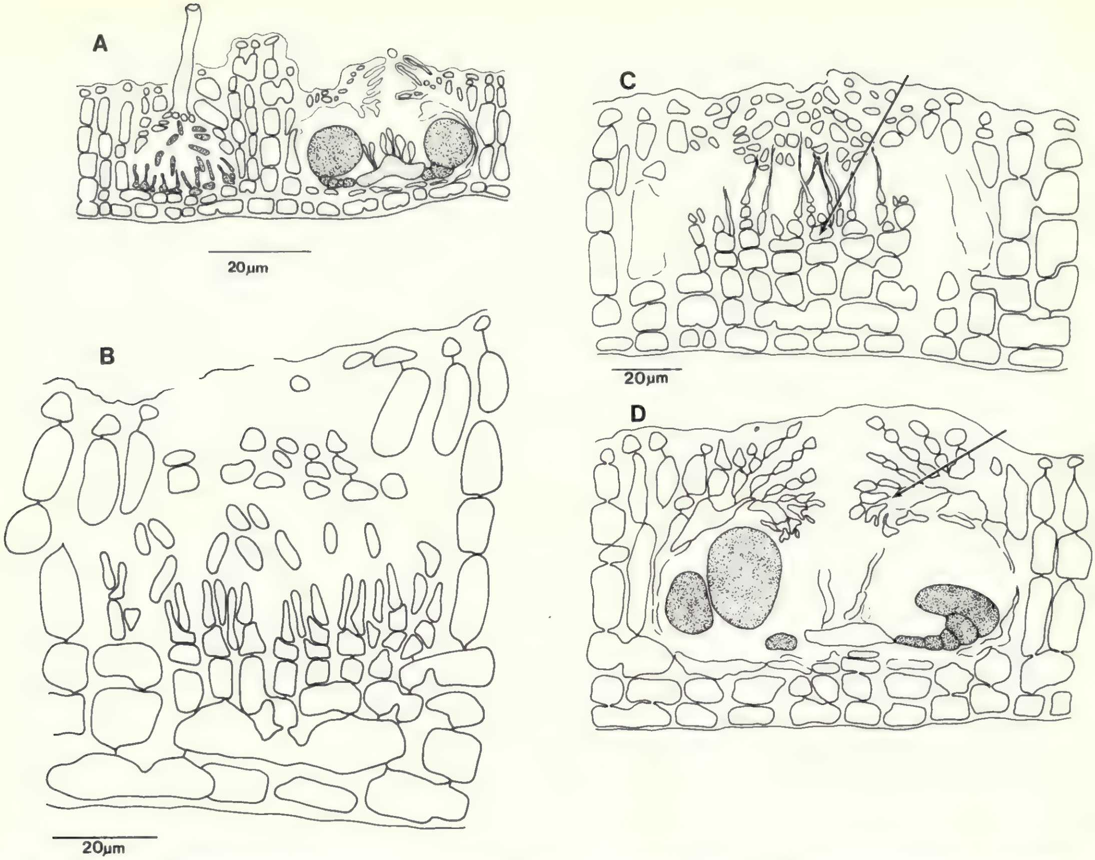

Fig. 71 Vertical sections of gametangial crusts of *Pneophyllum lobescens*. A, Spermatangial and adjacent carposporangial conceptacle. B, Spermatangial conceptacle. C, Mature carpogonial conceptacle showing bicarpogonial procarps (arrow). D, Mature carposporangial conceptacle showing the fusion cell with gonimoblast filaments and growth of ostiole filaments from perithallial cells (arrow).

Bisporangial plants: The development and structure of bisporangial conceptacles and ostioles (Figs 67D; 68E; 70C, D; 72C) is the same as for tetrasporangial conceptacles. The plump, oval bisporangia are also very numerous, and, when mature, burst out of the conceptacle when it is sectioned (Fig. 70C).

Phenology: Collections from three areas have been seen of this species. In July 1973 subtidal bisporangial and gametangial material was collected in the Shetland Islands, in October 1977 material of all reproductive phases was collected on glass from the River Yealm at a depth of 8 m; while Batters collected gametangial plants from Plymouth in March and April. It is probable that the species grows throughout the year subtidally but in the laboratory growth and reproduction were slower in winter than in summer (Chamberlain, 1982).

Form range: In laboratory culture, crusts grown in winter tend to be in poor condition, to have much more lobed edges, and more elongated cells than the smoother, more regular crusts, with large, more or less square cells, seen under warm but shaded summer conditions. Trichocytes (Figs 67G, 69B) occur abundantly in summer and may occasionally be present, particularly in an immature form, throughout the winter (Chamberlain, 1982).

Distribution:
British Isles: Devon, Shetland Is.

HABITAT: This species is so far known only from glass fragments, stones and razor shells collected from the subtidal zone.

LIFE HISTORY: A regularly alternating *Polysiphonia*-type life history and a self-perpetuating bisporangial life history have both been demonstrated in laboratory culture. The time taken to complete life history phases varies with environmental conditions (Chamberlain, 1982).

Table 24 Dimensions of vegetative structures (in µm unless stated).

Pneophyllum lobescens		British Isles
crust diameter		up to *c.* 10 mm
crust depth		*c.* 90
crust cell surface	length	(6·5) 12 (16·5)
	width	(4·5) 8 (11)
crust cell	height	
epithallial cell surface view	length	(3) 4 (4·5)
	width	(4·5) 6·5 (11)
epithallial cell	height	*c.* 7
hypothallial cell VS	width	(5) 13 (25)
	height	4–9
perithallial cell VS	width	(8) 10 (16)
	height	(8·5) 13 (23)
	number	up to 6
trichocyte type		intrafilament and branch cell
trichocyte surface view	length	11·5–13
	width	10–14·5

RIDGWAY COLOUR CODE:
dry crust – vinaceous lilac, pl. XLIV
tourmaline pink, pl. XXXVIII (lower surface)
fresh crust – deep corinthian red, pl. XXVII

10. Pneophyllum plurivalidum Y. Chamberlain, sp. nov.

HOLOTYPE: BM! Y. M. Chamberlain no 77/228, 29 October 1977, mouth of River Yealm, south Devon, at a depth of 8 m. Culture slide no 104/21 (Fig. 73A) grown from spores from this original collection.

DIAGNOSIS: Species epilithica perithallio profundo: a *P. lobescenti* differt cellulis longis sinuosis et a *P. zonali* conceptaculis immersis sine filamentis ostiolaribus.

DESCRIPTION: Crustae leaves, roseae ad sanguineae, diametro usque ad 60 mm, profunditate 100 µm, perithallium media in crusta profunditate usque ad 8 cellulas, *cellulae perithallii* (in sectione verticali) 6–18·5 µm latae × 7·5–15 µm altae, margo crustae ex hypothallio et epithallio modo constatus, *cellulae crustae* aspectu superficiali elongatae, sinuosae, 12·5–22·5 µm longae × 2–8 µm latae, *cellulae epithallii* 3·5–9 µm longae × 1·5–6 µm latae, *trichocytis* intra filamenta bulbosis amplitudine cellulae crustae simili; conceptacula immersa, omnia, praeter ea spermatangialia, ostiolis tholiformibus, *conceptacula carposporangialia* diametro interno 65–81 µm, altitudine 39–73 µm, *conceptacula spermatangialia* immersa, diametro 39–52 µm, altitudine 26–42 µm, ostiolo in canalem producto, *conceptacula tetrasporangialia* incognita, *conceptacula bisporangialia* diametro interno 104–117 µm, altitudine 65–81 µm, usque ad 16 bisporangii in unoquoque conceptaculo, bisporangia peripheralia, 36·5–47 µm longa × 23·5–31 µm lata.

DIAGNOSIS: Epilithic species with deep perithallium; differing from *P. lobescens* in having long, sinuous crust cells and from *P. zonale* in having immersed conceptacles which lack ostiolar filaments.

Table 25 Dimensions of reproductive structures (μm unless stated).

Pneophyllum lobescens	British Isles
CARPOSPORANGIAL CONCEPTACLE	
external diameter	
surface diameter	(88) 105 (130)
VS internal diameter	(88) 99 (112)
VS height	(46) 60 (68)
VS roof height	(13) 21 (26)
roof type	uniform
no. basal cell rows	1–2
ostiole	domed
no. gonimoblast filaments	*c.* 14–18
diameter carpospore	
SPERMATANGIAL CONCEPTACLE	
VS/surface width	34–52
VS height	35–48
length spermatium	6–8·5
width spermatium	2–3·5
TETRASPORANGIAL CONCEPTACLE	
external diameter	
surface diameter	(100) 122 (164)
VS internal diameter	(104) 120 (138)
VS height	(65) 76 (91)
VS roof height	(15) 20 (26)
roof type	uniform
no. basal cell rows	1–2
ostiole	domed
no. tetrasporangia	up to *c.* 18
length tetrasporangium	(43) 51 (54·5)
width tetrasporangium	(24·5) 30 (41·5)
BISPORANGIAL CONCEPTACLE	
external diameter	
surface diameter	(91) 117 (143)
VS internal diameter	(82) 109 (138)
VS height	(59) 69 (93)
VS roof height	(8) 17 (26)
roof type	uniform
no. basal cell rows	1–3
ostiole	domed
no. bisporangia	up to *c.* 20
length bisporangium	(36·5) 42·5 (51)
width bisporangium	(19·5) 26 (35)

DESCRIPTION: Smooth, reddish-pink to brown crusts up to 60 mm diameter, 100 μm deep, perithallium up to 8 cells deep centrally, *perithallial cells* (in VS) 6–18·5 μm wide × 7·5–15 μm high, crust border composed of hypothallium and epithallium only, *crust cells* in surface view elongated, sinuous, 12·5–22·5 μm long × 2–8 μm wide, *epithallial cells* 3·5–9 μm long × 1·5–6 μm wide, bulbous intrafilament *trichocytes* of similar size to crust cells; conceptacles immersed, all except spermatangial conceptacles with dome-like ostioles, *carposporangial conceptacles* 65–81 μm internal diameter × 39–73 μm high, *spermatangial conceptacles* immersed, 39–52 μm diameter × 26–42 μm high with ostiole prolonged into a spout; *tetrasporangial conceptacles* unknown, *bisporangial conceptacles* 104–117 μm internal diameter × 65–81 μm high, bisporangia peripheral, 36·5–47 μm long × 23·5–31 μm wide, up to 16 per conceptacle.

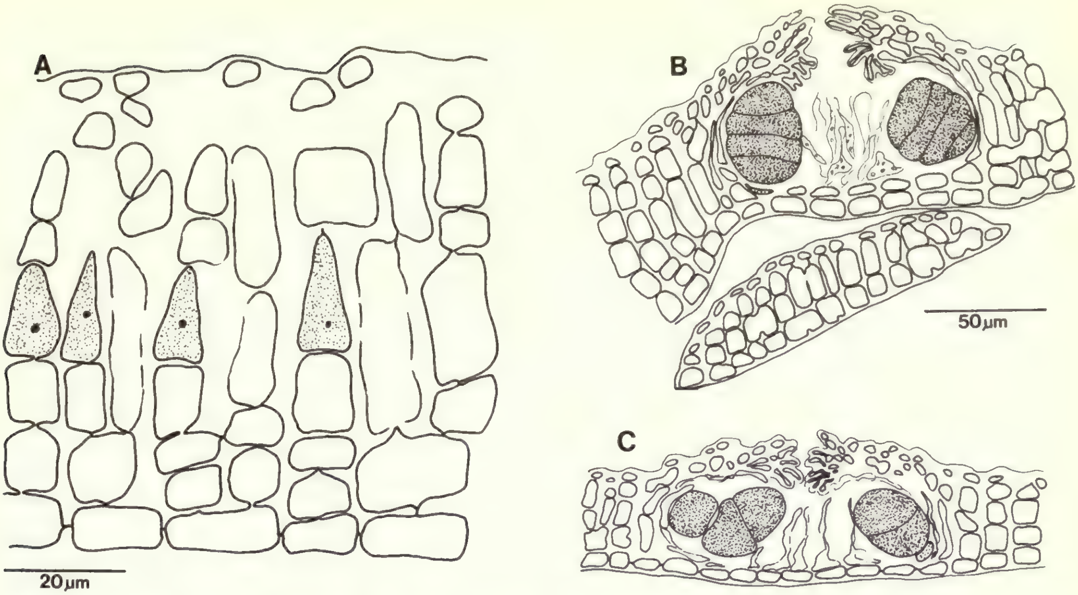

Fig. 72 Vertical sections of tetra- and bisporangial conceptacles of *Pneophyllum lobescens*. A, Young tetrasporangial conceptacle showing tetrasporangia (shaded) developing between sterile cells. B, Mature tetrasporangial conceptacle with central sterile paraphyses. This also shows two superimposed crusts. C, Mature bisporangial conceptacle with central sterile paraphyses.

HISTORICAL: *P. plurivalidum* is a long-lived epilithic species when grown in laboratory culture (Chamberlain, 1982). The same taxon was collected by Mme Lemoine from the glass of the aquarium tanks at the marine station at Roscoff, Brittany in August 1912 (PC) and identified as *Melobesia zonalis*. When I collected crusts from the same tanks in June 1979 only *Fosliella farinosa* and *Pneophyllum myriocarpum* were observed.

P. plurivalidum appears to be similar to *Fosliella valida* (Adey & Adey, 1973). Both have a deep crust (Fig. 73C) and the immersed conceptacles are of a similar size (Tab. 27), but the perithallial cells of *F. valida* are much smaller than those of *Pneophyllum plurivalidum*. No details regarding the shape of the thallus cells in surface view or conceptacle structure and surface features are available for *Fosliella valida*.

CRUST APPEARANCE: In laboratory culture (Chamberlain, 1982) *P. plurivalidum* forms substantial (up to 100 µm deep), epilithic crusts (Figs 73A; 74A) which are pinkish-red to dense brownish-purple, becoming darker in the older parts. The crusts are strongly adherent and usually have a smooth, regular periphery which does not become lobed. Crusts have grown to 60 mm diameter to date. The centre of older crusts becomes loosened and finally detaches.

Under the S.E.M. (Fig. 75C) the crust cells are elongated with relatively large, rounded-rectangular, epithallial concavities. The cells are broadest at the epithallial concavity, which gives them a characteristically wavy outline. Intrafilament trichocytes occur (Fig. 75D); they appear swollen relative to adjacent cells and the epithallial concavity is absent. The lower surface of the crust (Fig. 75F) shows flattened filaments with circular holes at intervals.

The conceptacles are immersed in the thallus (Figs 74C, D; 75E), but may become prominent in older dried material (Figs 74A, B). The conceptacle roof (Fig. 74 C, D) is smooth except in the immediate vicinity of the ostiole in younger conceptacles, while the thallus surface is irregularly shed in older conceptacles (Fig. 74B), when the ostiole dome (Figs 75A, B) becomes surrounded by rounded cells with large epithallial concavities.

VEGETATIVE ANATOMY: In culture the crusts have a border composed of hypothallial and epithallial cells only, but this is probably not usually visible in shore-collected specimens. The

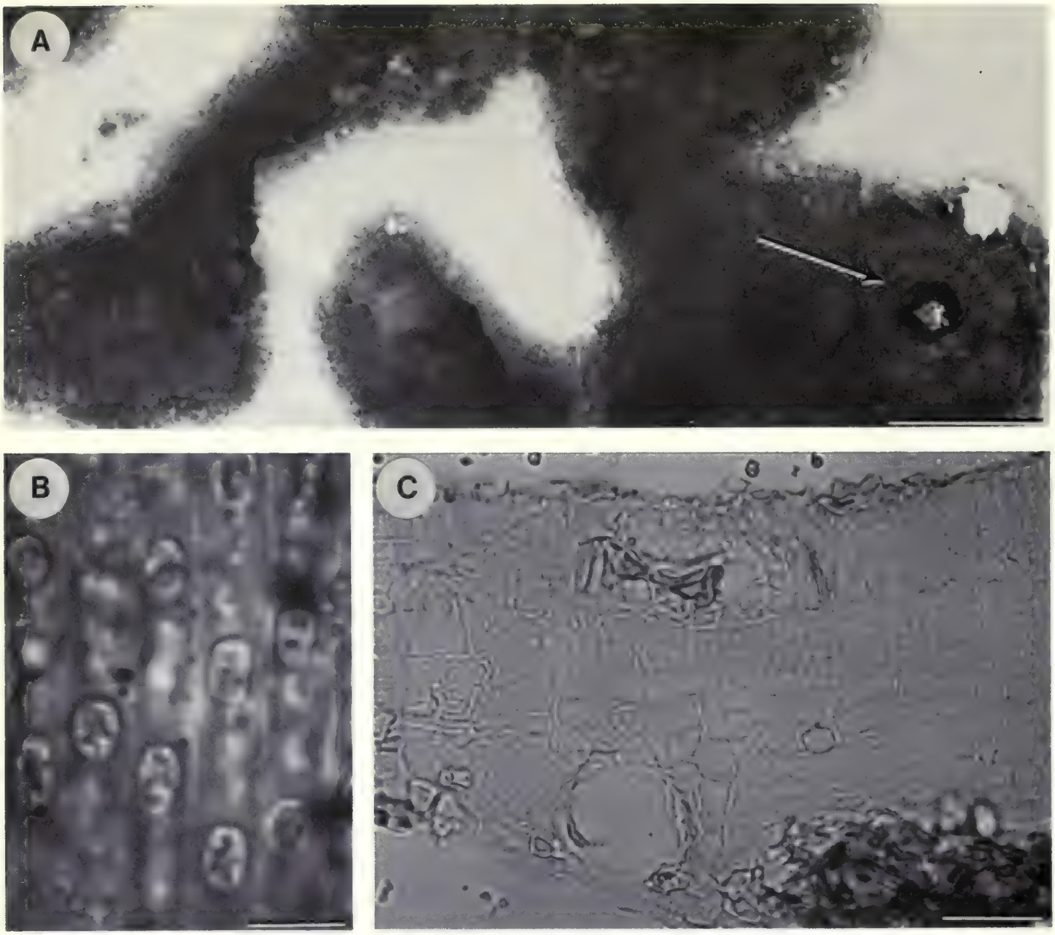

Fig. 73 Vegetative features of *Pneophyllum plurivalidum* and *Fosliella valida*. A, Type specimen of *Pneophyllum plurivalidum* with bisporangial and gametangial (arrow) crusts. Scale = 5 mm. B, Surface view of *Pneophyllum plurivalidum* crust showing elongated crust cells and large, oval, epithallial cells. Scale = 10 µm. C, Vertical section of *Fosliella valida* (Adey slide no. 70-2 10-30C 4) showing small, more or less isodiametric perithallial cells and edge of a carposporangial conceptacle. Scale = 25 µm.

crust cells are long and narrow (Fig. 73B), and the epithallial cells are radially ovate in surface view and domed in vertical section. Intrafilament trichocytes are present but are not divided into a pigmented and non-pigmented parts so that they are difficult to locate except by the absence of an epithallium in decalcified crusts; they are of the same order of size as the crust cells. A perithallium up to eight cells deep develops, the cells of which vary from being more or less isodiametric to vertically elongated in VS (Figs 75E; 76A, B; 77). The perithallial cells usually contain floridean starch grains (e.g. Figs 76B–E) which increase in quantity and size from the crust surface downward.

Gametangial plants: The crusts are monoecious with spermatangial conceptacles usually adjacent to carpogonial conceptacles (Figs 74A–C; 76B). The young spermatangial conceptacle (Fig. 77D) comprises a fertile disc at the base of the conceptacle bearing elongate cells; the mature conceptacle (Figs 76E; 77E) is globose and immersed in the thallus. Although the ostiole is prolonged into a spout, it is not very conspicuous in surface view (Figs 74B, C). Young carpogonial conceptacles (Fig. 77A) develop within the perithallium and, when mature (Figs 76C; 77B), the fertile disc in the centre of the conceptacle floor bears procarps. The central

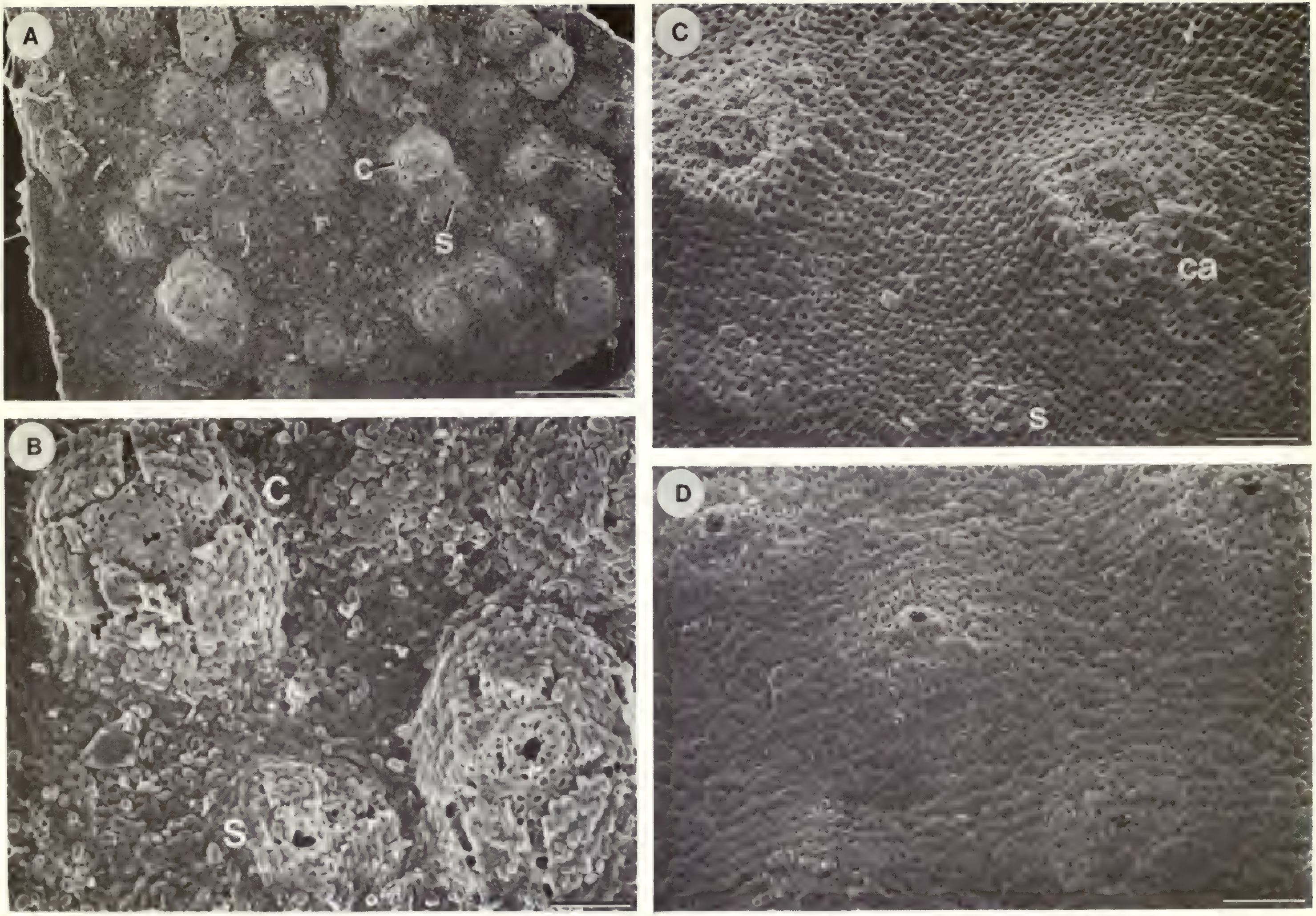

Fig. 74 Scanning electron micrographs of *Pneophyllum plurivalidum*. A, General view of mature gametangial crust showing carposporangial (c) and spermatangial (s) conceptacles. Scale = 250 μm. B, Enlarged view of A showing carposporangial (c) and spermatangial (s) conceptacles. Scale = 100 μm. C, Young gametangial crust showing carpogonial (ca) and spermatangial (s) conceptacles. Scale = 100 μm. D, Bisporangial crust with heavy diatom cover. Scale = 100 μm.

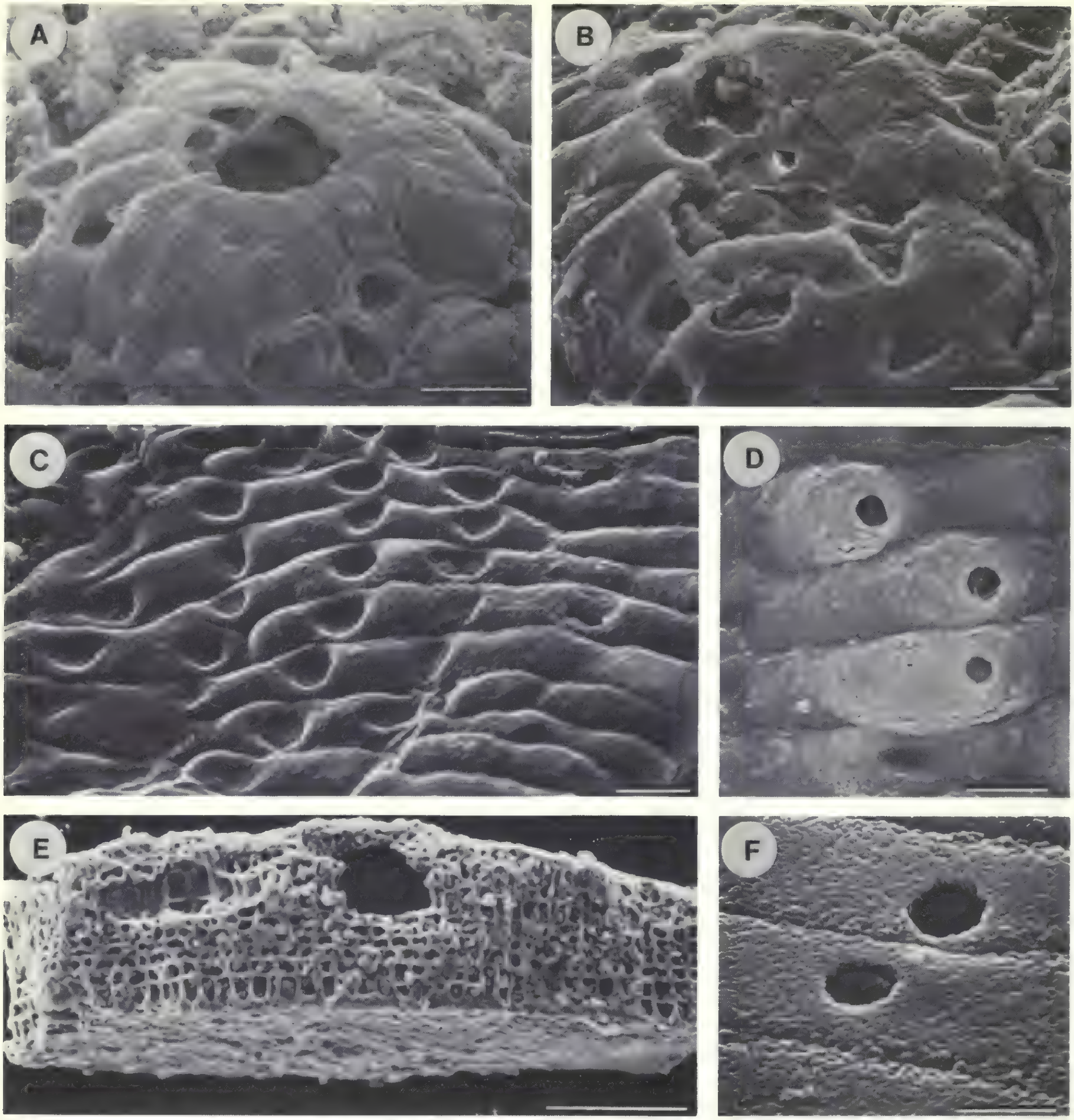

Fig. 75 Scanning electron micrographs of *Pneophyllum plurivalidum*. A, Bisporangial ostiole. Scale = 10 μm. B, Carposporangial ostiole. Scale = 10 μm. C, Crust cells. Scale = 10 μm. D, Trichocytes. Scale = 10 μm. E, Vertical fracture of bisporangial crust. Scale = 100 μm. F, Lower surface of thallus showing 'pores'. Scale = 5 μm.

procarps bear one or two carpogonial branches, each with long trichogynes (Figs 76C; 77B). The fertile area is surrounded by vertically stretched perithallial cells which initiate roof and ostiolar filaments apically; as these filaments develop they start to push off the original thallus surface (Figs 76C; 77A).

Carposporangial plants: As the carposporangial conceptacles mature, the stretched perithallial cells disintegrate and the original thallus surface is sloughed off round the ostiole (Figs 76D; 77C). The downward ostiolar filaments are short and somewhat swollen at the tip (Figs 76D; 77C), while the upward ostiolar filaments are short, but immediately round the ostiole they form a dome-like structure of broad cells (Figs 75B; 76D; 77C), the top parts of which break off as the ostiole ages (Fig. 75B). The fusion cell (Figs 76D; 77C) is quite small and deep, it is closely

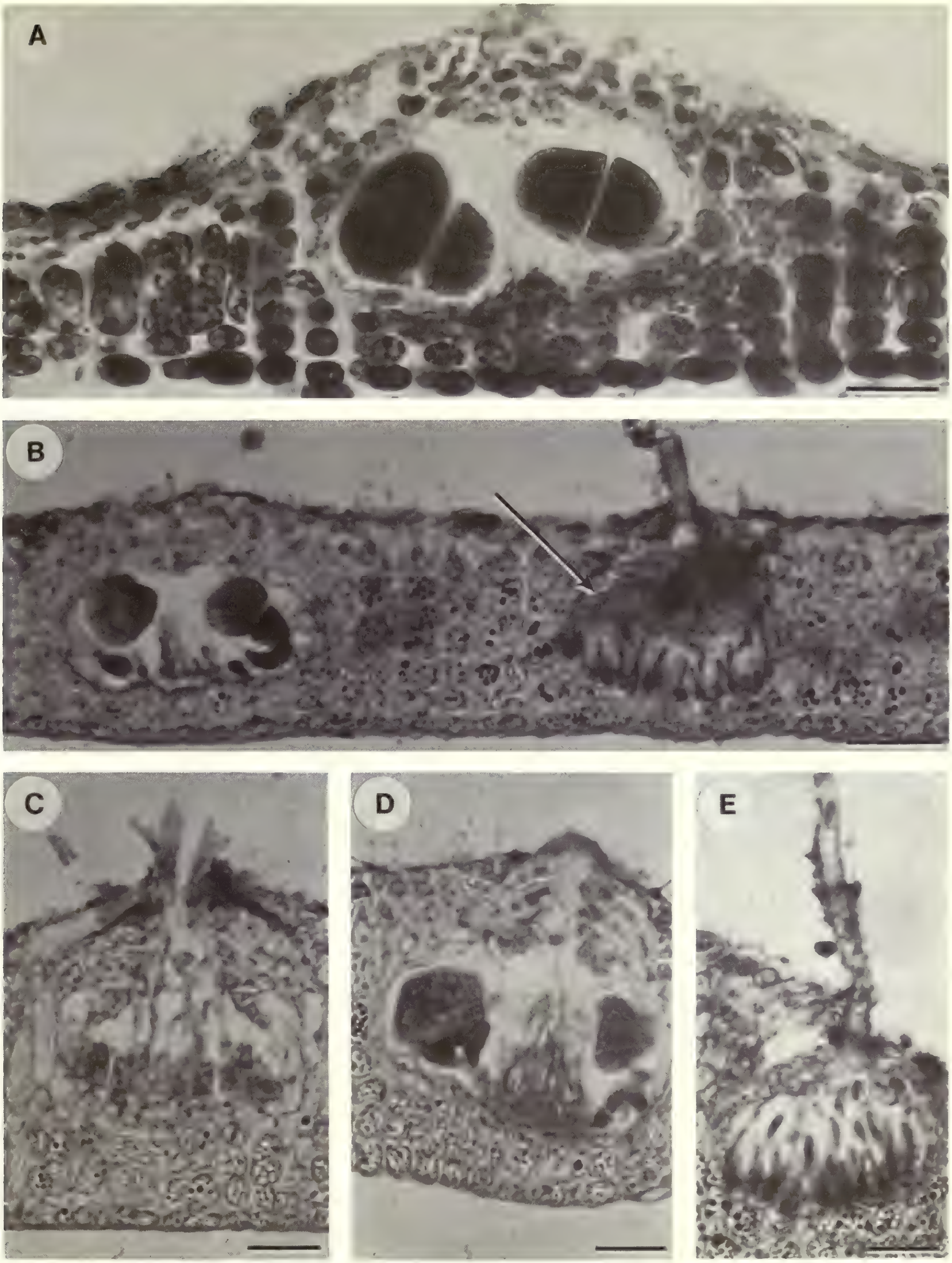

Fig. 76 Vertical sections of reproductive crusts of *Pneophyllum plurivalidum*. A, Bisporangial crust. Scale = 25 μm. B, Gametangial crust showing carposporangial and spermatangial (arrow) conceptacles. Scale = 25 μm. C, Carpogonial conceptacle. Scale = 10 μm. D, Carposporangial conceptacle. Scale = 10 μm. E, Spermatangial conceptacle. Scale = 10 μm.

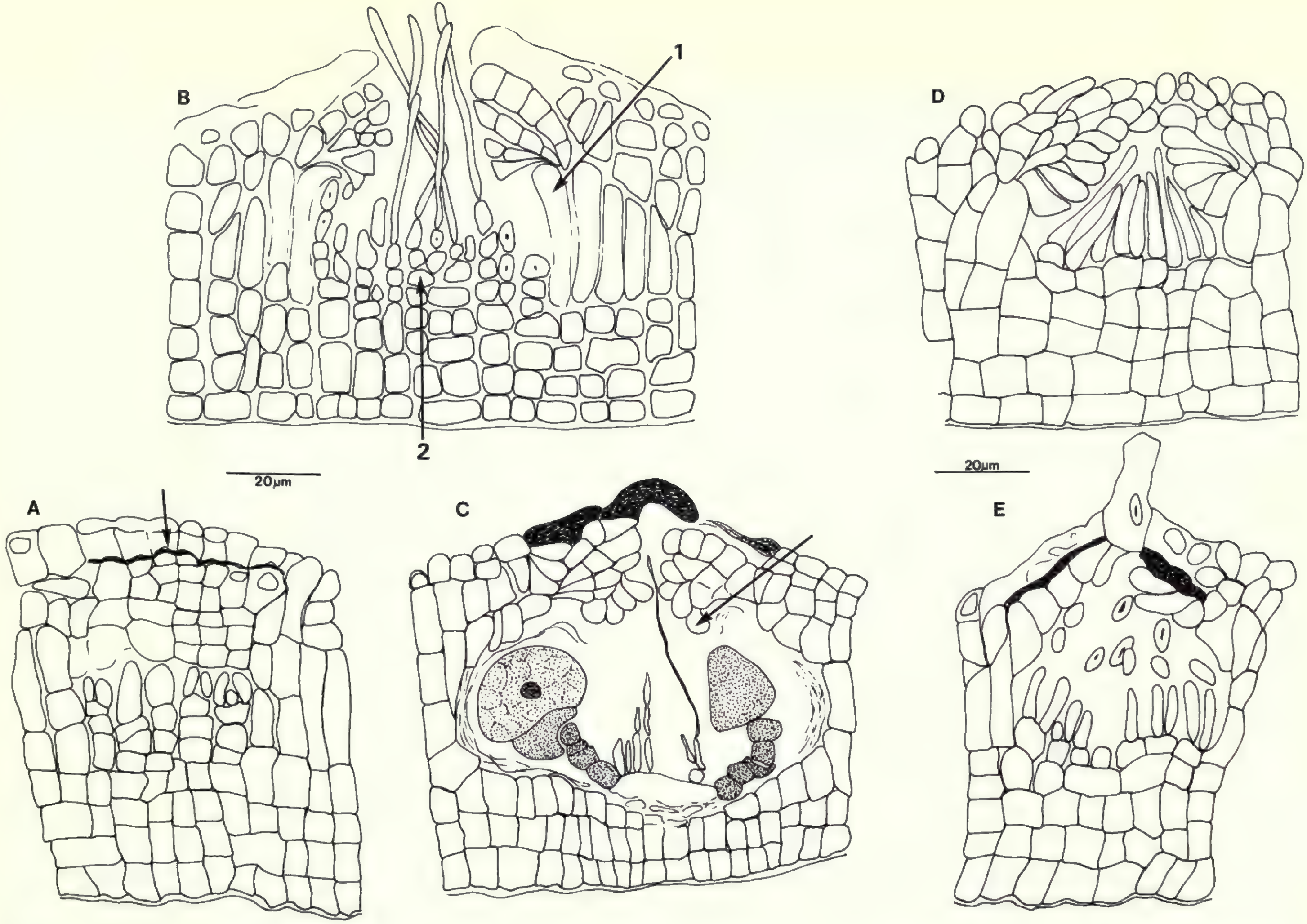

Fig. 77 Gametangial/carposporangial conceptacles of *Pneophyllum plurivalidum*. A, Vertical section of young carpogonial conceptacle showing new roof developing below the thallus surface (arrow). B, Vertical section of mature carpogonial conceptacle showing ostiole filaments developing from perithallial cell (1) and procarp bearing two carpogonia (2). C, Vertical section of carposporangial conceptacle with remains of thallus surface (black) and showing the swollen, downward ostiole filaments (arrow). D, Vertical section of young spermatangial conceptacle. E, Vertical section of mature spermatangial conceptacle.

appressed to the basal cells, and carposporangial filaments up to seven cells long are borne peripherally.

TETRASPORANGIAL PLANTS: Attempts to grow crusts initiated from carpospores are in progress; it is probable that these plants will be tetrasporangial.

BISPORANGIAL PLANTS: These are similar to the carposporangial plants (Figs 74D; 75A,E; 76A) and the conceptacle and ostiole development and structure follow the same pattern. The bisporangia (Fig. 76A) are borne peripherally on stalk cells; there is no development of sterile filaments or columella.

PHENOLOGY: Little information is available about the occurrence of this species in nature. In the laboratory, however, the crusts remained healthy throughout the winter, but grew and reproduced much more slowly at this season than during the summer (Chamberlain, 1982).

FORM RANGE: In crusts grown in the laboratory crust cells are noticeably shorter and broader [(5) 8·5 (9·5) μm long × (5) 6·5 (8) μm wide] in winter conditions than the characteristically elongated cells seen under favourable conditions. Trichocytes are present under warm, well-illuminated conditions, but absent in colder darker conditions (Chamberlain, 1982); very large, irregular crust cells and trichocytes are seen occasionally as in *P. myriocarpum*.

DISTRIBUTION:
British Isles: Devon.
World: France (Brittany).

HABITAT: Known only on fragments of glass collected from the subtidal zone and the glass walls of aquarium tanks.

LIFE HISTORY: A self-perpetuating, bisporangial life history has been demonstrated. The time taken to complete life history phases varies with environmental conditions (Chamberlain, 1982).

Table 26 Dimensions of vegetative structures (in μm unless stated).

Pneophyllum plurivalidum	British Isles	Adey & Adey (1973) *Fosliella valida*
crust diameter	up to 60 mm	
crust depth	up to 100	*c.* 70
crust cell length	(12·5) 17 (22·5)	7–14
surface width	(2) 6·5 (8)	5–9·5
crust cell height		
epithallial cell length	(3·5) 7 (9)	2·5–5·5
surface view width	(1·5) 4·5 (6)	3–8
epithallial cell height	(3) 4·5 (6)	
hypothallial cell width	(5·5) 11 (18·5)	
VS height	(5·5) 7 (8·5)	
perithallial width	(6) 10 (18·5)	2·5–6·5
cell height	(7·5) 10 (15)	3·5–8·5
VS number	up to 8	up to 7 or more
trichocyte type	intrafilament	rare
trichocyte length	as crust cells	
surface view width	as crust cells	

RIDGWAY COLOUR CODE: dry crust – deep purplish vinaceous, pl. XLIV
fresh crust – hydrangea red, pl. XXVII

11. Pneophyllum zonale (P. Crouan & H. Crouan) Y. Chamberlain, **comb. nov.**

BASIONYM: *Hapalidium zonale* P. Crouan & H. Crouan in *Annls Sci. nat.* (Bot.) IV, **12**: 284 Pl. 21, Fig. A(1–7) (1859) (see Fig. 44A of present study).

Table 27 Dimensions of reproductive structures (μm unless stated).

Pneophyllum plurivalidum	British Isles	Adey & Adey (1973) *Fosliella valida*
CARPOSPORANGIAL CONCEPTACLE		
external diameter		
surface diameter	(70) 78 (86)	
VS internal diameter	(65) 73 (81)	(77) 89 (95)
VS height	(39) 54 (73)	(37) 43 (47)
VS roof height	(13) 19 (26)	(10) 13 (15)
roof type	irregular	
no. basal cell rows	2–3	
ostiole	domed	
no. gonimoblast filaments	*c.* 9	
diameter carpospore		
SPERMATANGIAL CONCEPTACLE		
VS/surface width	(39) 45 (52)	(47) 53 (57)
VS height	(26) 33 (42)	(25) 27 (30)
length spermatium	(4·5) 7 (9·5)	
width spermatium	(2) 2·5 (3·5)	
TETRASPORANGIAL CONCEPTACLE		
external diameter		
surface diameter		
VS internal diameter		(75) 87 (100)
VS height		(55) 60 (77)
BS roof height		(12) 14 (16)
roof type		
no. basal cell rows		
ostiole		
no. tetrasporangia		
length tetrasporangium		
width tetrasporangium		
BISPORANGIAL CONCEPTACLE		
external diameter		
surface diameter	(78) 110 (130)	
VS internal diameter	(104) 113 (117)	
VS height	(65) 76 (81)	
VS roof height	(13) 16 (21)	
roof type	smooth to irregular	
no. basal cell rows	2–4	
ostiole	domed	
no. bisporangia	up to *c.* 16	
length bisporangium	(36·5) 43 (47)	
width bisporangium	(23·5) 27 (31)	

NOMENCLATURAL SYNONYMS: *Melobesia* (subgenus *Eumelobesia*) *zonalis* (P. Crouan & H. Crouan) Foslie in *K. nor. Vidensk. Selsk. Skr.* **1898** (3): 11 (1898).

Melobesia (subgenus *Heteroderma*) *zonalis* (P. Crouan & H. Crouan) Foslie in *K. nor. Vidensk. Selsk. Skr.* **1899** (7): 4 (1900 ['1899']).

Lithophyllum (subgenus *Carpolithon*) *zonale* (P. Crouan & H. Crouan) Foslie in *K. nor. Vidensk. Selsk. Skr.* **1905** (5): 9 (1905).

Lithophyllum (subgenus *Pliostroma*) *zonale* (P. Crouan & H. Crouan) Foslie in *K. nor. Vidensk. Selsk. Skr.* **1908** (7): 20 (1908).

Melobesia (subgenus *Pliostroma*) *zonalis* (P. Crouan & H. Crouan) Foslie in *K. nor. Vidensk. Selsk. Skr.* **1908** (11): 4 (1908) – forma *typica* [Foslie (1908*b*) said that Foslie (1908*a*) should have read *Melobesia* (*Pliostroma*) *zonalis* not *Lithophyllum*].

Heteroderma (subgenus *Pliostroma*) *zonale* (P. Crouan & H. Crouan) Foslie in *K. nor. Vidensk. Selsk. Skr.* **1909** (2): 56 (1909).
Fosliella (subgenus *Pliostroma*) *zonalis* (P. Crouan & H. Crouan) Feldmann in *Rev. algol.* **11**: 317 (1942 ['1939']).
Fosliella (subgenus *Heteroderma*) *zonalis* (P. Crouan & H. Crouan) Bressan in *Boll. Soc. adriat. Sci. nat.* **59**: 398 (1974).
Fosliella zonalis (P. Crouan & H. Crouan) Ganesan (sic); Parke & Dixon in *J. mar. biol. Ass. U.K.* **56**: 534 (1976).

References: *Hapalidium zonale* P. Crouan & H. Crouan; P.-L. and H.-M. Crouan, *Florule de Finistère*: 149 (1867); Foslie in *K. nor. Vidensk. Selsk. Skr.* **1899** (7): 4 (1900 ['1899']).
Melobesia (subgenus *Heteroderma*) *zonalis* (P. Crouan & H. Crouan) Foslie; Foslie in *K. nor. Vidensk. Selsk. Skr.* **1900** (5): 21 (1900).
Melobesia (subgenus *Pliostroma*) *zonalis* (P. Crouan & H. Crouan) Foslie; Hamel and Lemoine in *Archs Mus. natn. Hist. nat. Paris* VII, **1**: 108 (1953 ['1952']) – excluding Fig. 77; Feldmann in *Trav. Stn. biol. Roscoff*, suppl. **6**: 79 (1954).
Melobesia zonalis sensu Newton, *A handbook of British seaweeds*: 302 (1931) – pro parte.
Melobesia trichostoma Rosenv. in *K. danske Vidensk. Selsk. Skr.* VII, **7**: 253 (1917).
Fosliella tenuis Adey & Adey in *Br. phycol. J.* **8**: 398 (1973) (as to Pl. XIV and slide 78-1650-70E; description possibly includes *Pneophyllum myriocarpum*).

Excluded records: *Melobesia* (subgenus *Pliostroma*) *zonalis* sensu Lemoine in *Archs Mus. natn. Hist. nat. Paris* V, **5**: 140 Fig. 7 (1913) (= *Fosliella farinosa*), in *Bull. Lab. marit. Mus. Hist. nat. St. Servan* **7**: 20 (1931) (= *Pneophyllum myriocarpum*); Hamel and Lemoine in *Archs Mus. natn. Hist. nat. Paris* VII, **1**: Fig. 72 (1953 ['1952']) (= *Fosliella farinosa*).

Various other *Pneophyllum* species described or referred to by the Crouan brothers have been quoted (e.g. by Hamel & Lemoine, 1953, p. 108 and Bressan, 1974, p. 77) as synonyms of *P. zonale*. Examination of the Crouan collection (CO) showed that most of the samples on which these species were based were either epiphytes or such a mixture of epilithic crusts that it seems preferable to exclude them from the synonymy. They comprise:
Hapalidium coccineum P. Crouan & H. Crouan in *Annals Sci. nat. Bot.* IV, **12**: 285 (1859) (= *Melobesia membranacea*).
Hapalidium phyllactidium sensu P. Crouan & H. Crouan in *Annls Sci. nat. Bot.* IV, **12**: 286 (1859) – changed to *H. confervoides* in P. and H. Crouan, *Florule du Finistere*: 149 (1867) (= mixture of epilithic crusts).
Hapalidium roseum sensu P. Crouan & H. Crouan, *Florule du Finistère*: 149 (1867) (= mixture of epilithic crusts including *Pneophyllum zonale*).
Hapalidium callithamnioides P. Crouan & H. Crouan, *Florule du Finistère*: 149 (1867) (= *Pneophyllum confervicolum* f. *minutulum* q.v.).
Melobesia myriocarpa P. Crouan & H. Crouan, *Florule du Finistère*: 150 (1867) (= *Pneophyllum myriocarpum*).

Lectotype: CO! Herb. P.-L. & H.-M. Crouan, 24 January 1859, Rade de Camaret (dredged), France (Figs 78A, B, D). Chamberlain slide no. 1383.

Diagnosis: Plants mainly epilithic or epizoic, sometimes epiphytic, from intertidal pools or subtidal, with perithallium up to 8 cells deep and conceptacles with long, flattened ostiolar filaments: differing from *P. lobescens, P. plurivalidum* and *P. myriocarpum* in having larger conceptacles with ostiolar filaments, and from *P. rosanoffii* and *P. limitatum* in having larger conceptacles with a deeper roof of smaller cells and flattened ostiolar filaments.

Description: Dull, reddish or mauvish-pink crusts up to a few millimetres in diameter, 170 μm deep, often superimposing, frequently mixed with other species, perithallium up to 8 cells deep in crust centre, crust border of hypothallium and epithallium only (at least in cultured material), *perithallial* cells (in VS) 7–14·5 μm wide × 10–28·5 μm high; *crust cells* in surface view broadly rectangular, 10–17 μm long × 5–13·5 μm wide; *epithallial cells* 3·5–6·5 μm long × 4–9·5 μm wide, intrafilament and branch cell *trichocytes* 20–30 μm long × 11–14 μm wide; conceptacles gently raised, all except spermatangial conceptacles with long, wispy ostiolar filaments, *carposporangial conceptacle* (one only) 135 μm internal diameter × 73 μm high, *tetrasporangial*

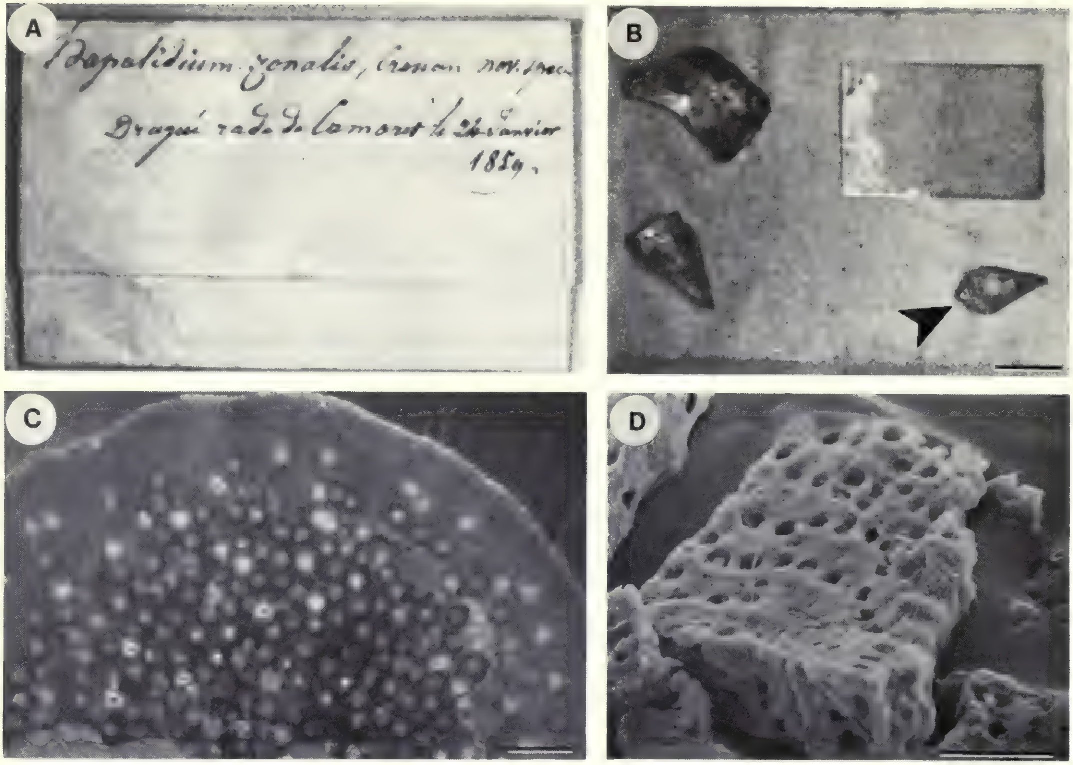
A
Hapalidium zonalis, Crouan nov. spec.
Dragué rade de Lamort le 24 Janvier
1859.
B
C
D

Fig. 78 Type material and crust appearance of *Pneophyllum zonale.* A, Packet containing the type specimen. B, Packet opened: the lectotype crust of *Hapalidium zonale* P. Crouan & H. Crouan is on the smallest piece of glass (arrow). Scale = 10 mm. C, Bisporangial crust of *Pneophyllum zonale* grown in laboratory culture. Scale = 1 mm. D, Type crust showing thallus surface. Scale = 25 μm.

conceptacle 156–240 μm internal diameter × 78–99 μm high, tetrasporangia 49·5–74 μm long × 26–41·5 μm wide, *bisporangial conceptacles* 96–260 μm internal diameter × 65–117 μm high, up to about 60 bisporangia per conceptacle, 41·5–73 μm long × 26–34 μm wide.

HISTORICAL: Because of the technical difficulty in examining epilithic simple crustose corallines the identity of the Crouan brothers' (1859) *Hapalidium zonale* has hitherto remained somewhat vague and the specific epithet has been generally applied to many simple epilithic crusts. However, when dimensions and descriptions have been given, they have usually indicated that a crust of up to 7–8 cells deep with large conceptacles (*c.* 300 μm diameter) are features regarded as typical of this taxon (e.g. Feldmann, 1942; Hamel and Lemoine, 1953; Bressan, 1974). Examination of the Crouans' herbarium in Concarneau revealed three collections labelled *Hapalidium zonale* by the Crouans. One collection is undated (Fig. 1) and displayed with the drawings as in the published description (P.-L. and H.-M. Crouan, 1859), whilst the other two are dated 1859 and 1862 respectively. The Crouans (1859) cited material collected up to and including January 1859 (p. 301) and it is from the collection dated 1859 that the lectotype (Figs 78A, B, D) has been selected. The collection comprises a packet containing a piece of mica on which nothing can be seen and three pieces of glass bearing a number of small, calcareous crusts. These crusts belong to various taxa. There is, however, one distinct and thicker tetrasporangial crust (Fig. 78B arrowed) which corresponds well with the Crouans' illustration (see Fig. 44A) of the crust cells, conceptacle, and tetrasporangium of *H. zonale.* Scanning electron micrographs (Fig. 78D) show this crust to have a deep thallus and elongated crust cells; the conceptacles are somewhat raised and measurements of conceptacles and cells, made on a decalcified whole mount, are shown in Tables 28 and 29.

Picquenard (1912*b*) published a catalogue of the red algae of the Crouan herbarium in which he gave the following references for *H. zonale*: '*H. phyllactidium* Crouan excl. synon.; *H. confervoides* Crouan excl. synon. (non Batters), *Melobesia myriocarpa* Crouan'. Of these names *M. myriocarpa* is a separate species (see *Pneophyllum myriocarpum*), while the *Hapalidium phyllactidium* (syn. *H. confervoides*) collections in Herb. Crouan show a mixture of crust types probably belonging to several species (see also under *Pneophyllum confervicolum*).

Foslie (1900*a*) discussed *Hapalidium zonale* on the basis of a Crouan collection sent to him from Paris. There are three such collections in Paris. One in Herb. Thuret is labelled Brest 1879, the other two are in the Herbier de France and are labelled as being 'ex Herb. Crouan' with a reference to the Crouans' (1859, 1867) publications. There is no indication as to which material Foslie received and his slide (TRH) has now dried out. Examination of one of the Herbier de France collections shows it to be young material of the present species. Foslie (1900*a*) described the Paris material of *Melobesia zonalis* as having a thallus only one or two cells deep with conceptacles 150–200 μm diameter seen from above which agrees better with *Pneophyllum myriocarpum* than *P. zonale* as now defined. On the other hand, Foslie (1900*a*) mentioned some crusts on glass, collected at 2–5 fathoms at Plymouth, which Batters sent him and which Foslie describes as having a thallus up to eight cells deep with conceptacles 150–200 μm from above. This is presumably the material identified by Batters as *Melobesia myriocarpa* (BM algal box collection no. 505) which is *Pneophyllum lobescens*. Foslie (1900*a*) also referred to some material collected by Batters at Plymouth growing on 'small shells of snails' which is presumably the collection on rissoid shells (BM algal box collection number 506) which is *Pneophyllum myriocarpum* (*q.v.*).

Lemoine's (1913) record and illustration of *P. zonale* (as *Melobesia*) from Clew Bay, Ireland, was based on *Fosliella farinosa*, material of which is in BM-K and DBN and shows superimposed bisporangial crusts. Rosenvinge's (1917) description and slides (C) of *Melobesia trichostoma* agree closely with the present description.

Pneophyllum zonale has most frequently been recorded from French localities and the records almost certainly represent more than one species. Lemoine (1931), for example, comments that material from the St Servan area (northern Brittany) was very thin and had conceptacles 175–200 μm diameter × 120–150 μm high. The material on which the St Servan records were based is in PC; unfortunately the crusts are so sparse that identification is not feasible, although Lemoine's description agrees well with *P. myriocarpum*.

The dimensions given by Bressan (1974) for Italian material agree with *P. zonale*.

Finally *Fosliella tenuis* Adey & Adey (1973) appears, from the written description, to be partly *Pneophyllum myriocarpum* (*q.v.*); however, the slide cited as being from the type specimen (67–16, 50–70E from Oslofjord) has been examined and it comprises sections of gametangial *P. zonale* with the characteristic *zonale* ostiole (Fig. 82E); the Adeys' illustrative diagram and table of dimensions (Adey & Adey, 1973, Tab. XIV) is also based on this entity and was prepared from the same slide (Norris & Townsend, 1981).

CRUST APPEARANCE: In culture (Chamberlain, 1982), crusts of *P. zonale* (Fig. 78C) grew to *c.* 10 mm diameter, and appeared brownish-pink with a border composed only of hypothallium and epithallium, which frequently became lobed because the crusts were growing on glass slides to which they did not adequately adhere. On the shore, individual crusts were most often seen on *Littorina*, *Patella*, and other shells in the intertidal zone, and such crusts were thick and brownish-mauve in colour. Layers of superimposed crusts as illustrated by Rosenvinge (1917) were not observed in the present investigation, but in cultured crusts it was noted that spores are often not liberated through the ostiole but released downwards when the bottom of the conceptacle falls out (Fig. 79B). The spores then germinate either on the substratum below the parent crust or on the under surface of the crust, and it is probably by this means that the crust layers are built up – with the older crusts eventually being pushed off by the younger ones below.

Under the S.E.M. (Fig. 79A) the crust periphery is seen to be composed of broadly rectangular cells with conspicuous, ovate epithallial concavities, intrafilament and branch cell trichocytes.

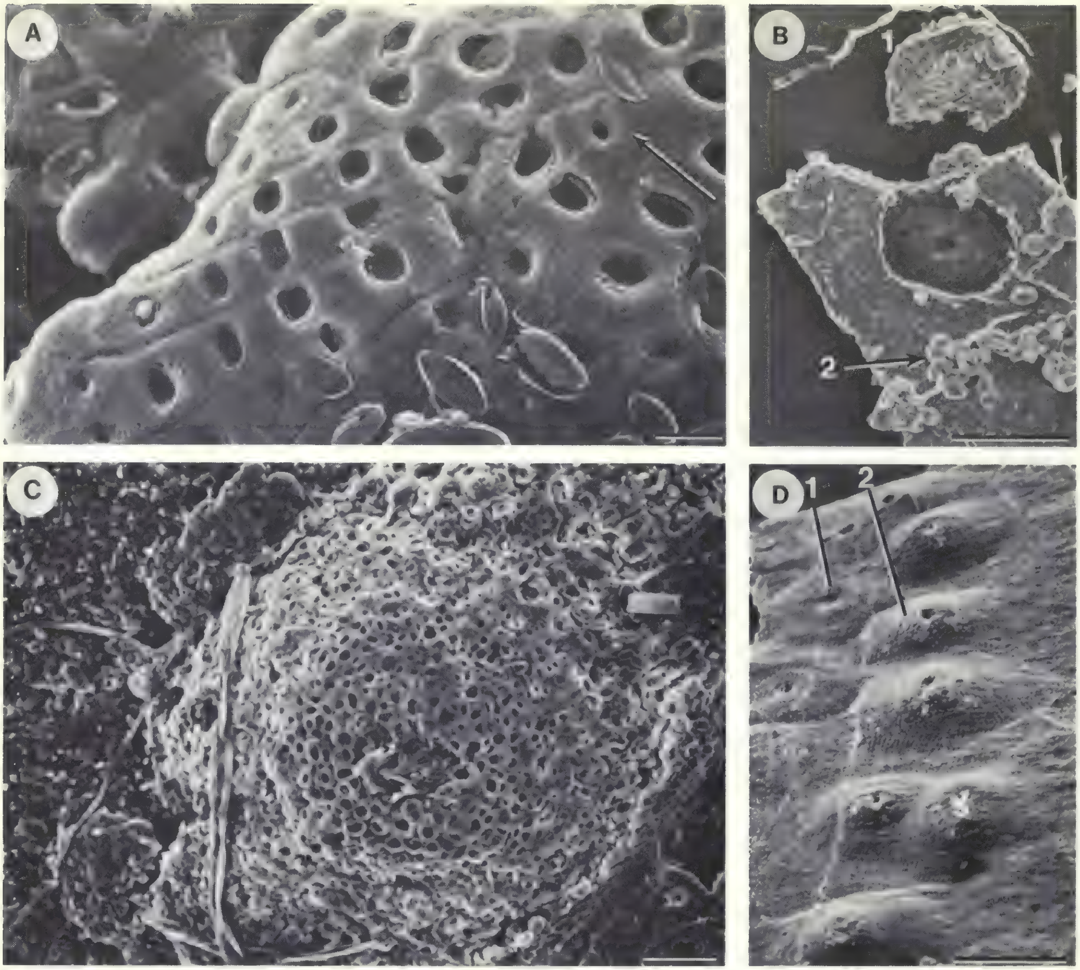

Fig. 79 Scanning electron micrographs of laboratory cultured bisporangial crusts of *Pneophyllum zonale*. A, Crust cells with trichocyte (arrow). Scale = 10 μm. B, Underside of crust showing detached conceptacle base (1) and sporelings (2) developing on lower crust surface. Scale = 500 μm. C, Senescent conceptacle. Scale = 50 μm. D, Young crust showing very early (1) and slightly later (2) conceptacle development. Scale = 500 μm.

In fresh and dried material the conceptacles appear gently rounded, and under the S.E.M. the conceptacle surface is uniform in young material (Fig. 79D), but the thallus surface cracks off irregularly in older conceptacles (Fig. 79C) to reveal the more or less isodiametric roof cells with large, central, epithallial concavities. The ostiole (Figs 80A–E) becomes surrounded by long, flat, papery-looking filaments in the mature conceptacle; in the early stages these filaments appear as a rim round the ostiole; when they start to elongate they are fused to each other and only become free when mature. In senescent conceptacles the filaments wither away.

Scanning electron micrographs of vertically fractured crusts show the deep conceptacle roof and perithallium (Fig. 80F).

Vegetative anatomy: The peripheral cells in cultured crusts (Fig. 81A) are broadly rectangular in surface view with conspicuous, more or less ovate epithallial cells, and the crust cells contain floridean starch grains. The perithallial filaments (Fig. 14) vary from being one to eight cells deep. Trichocytes (Fig. 81A) are frequent in summer months; they may occur within the filaments or in branch cells and are similar in size or somewhat larger than the surrounding crust

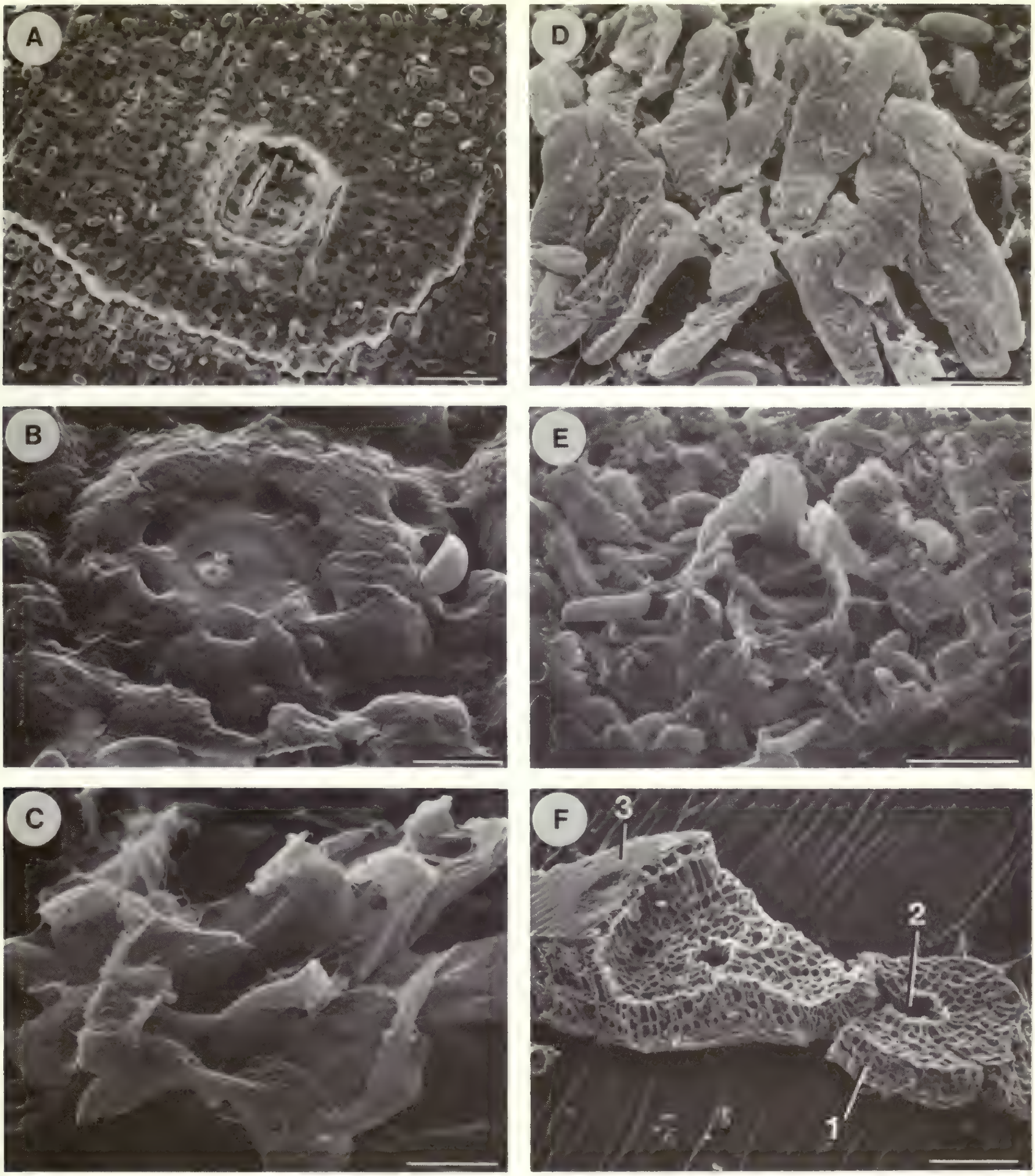

Fig. 80 Scanning electron micrographs to show conceptacle structure and stages in ostiole development in bisporangial crusts of *Pneophyllum zonale* grown in laboratory culture. A, Early stage of conceptacle growth shown as a depression in the thallus surface. Scale = 50 μm. B, Ostiole filaments beginning to surround ostiole depression. Scale = 10 μm. C, Ostiole filaments opened out but still fused. Scale = 10 μm. D, Mature ostiole filaments, critical point dried, showing flattened shape. Scale = 10 μm. E, Fused ostiole filaments starting to rise up. Scale = 25 μm. F, View from below of two adjacent conceptacles, showing deep conceptacle roof (1), ostiole in centre of underside of conceptacle roof (2), and lower surface of the thallus (3). Scale = 100 μm (both figures).

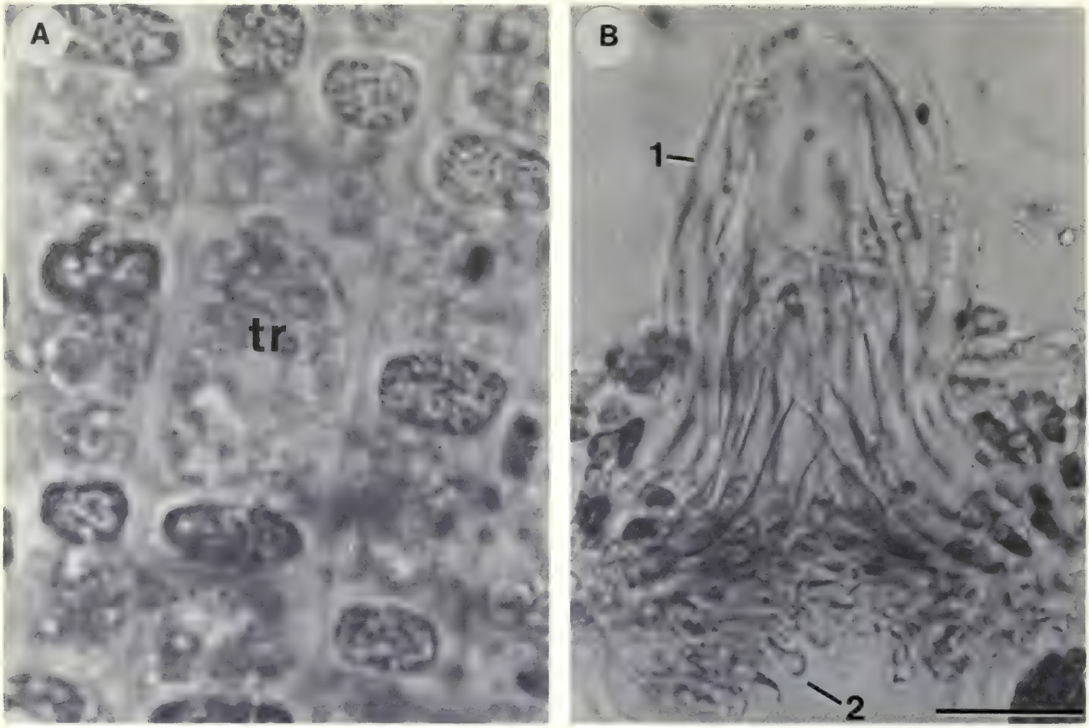

Fig. 81 Crust cells and characteristic ostiole filaments of *Pneophyllum zonale*. A, Crust cells with trichocyte (tr). B, Ostiole of bisporangial conceptacle showing upward (1) and downward-pointing (2) ostiole filaments. Scale = 10 μm.

cells. When mature they are divided by a radial wall into a pigmented part and a colourless, hair bearing part, and the epithallial cell is absent.

Gametangial plants: Only one gametangial plant, in poor condition, has been found in the present investigation; it was growing on *Chondrus crispus* at Bembridge on 6 February 1978. In VS it shows a young spermatangial conceptacle beside an empty, presumably carposporangial, conceptacle. From the descriptions and slides of Rosenvinge (1917, as *Melobesia trichostoma*) and Adey & Adey (1973, as *Fosliella tenuis*, see Fig. 82E) it is evident that the carposporangial and tetrasporangial conceptacles are similar to the bisporangial conceptacles in structure, and the bisporangial conceptacles will, therefore, be described in detail as they were the only type found in quantity in the present study.

Tetrasporangial plants: Tetrasporangial plants (Fig. 82D) have been found on only two occasions, at Bembridge and Anglesey, and both samples were growing on *Chondrus crispus*. The Anglesey conceptacles measure 216–240 μm internal diameter as compared with the Bembridge ones which measure 156–169 μm, but the overall size range is similar to that found for the bisporangial conceptacles. The tetrasporangia develop peripherally on stalk cells, and sterile paraphyses are present in the centre of the conceptacle (Fig. 14A).

Bisporangial plants: The young conceptacle is gently raised above the thallus surface (Figs 79D; 82A) with an internal cavity which is about twice as wide as high. The cultured conceptacles tend to be larger and more regularly formed than those of the shore material which are often humped and misshapen as were the tetrasporangial and carposporangial ones observed by Rosenvinge (1917). The conceptacle cavity develops by the vertical stretching (Fig. 82A) and eventual rupture of the perithallial cells. The roof filaments are initiated from the upper ends of the perithallial cells (Fig. 83) and form deep filaments of cells (Figs 14B; 80F; 82B), with small

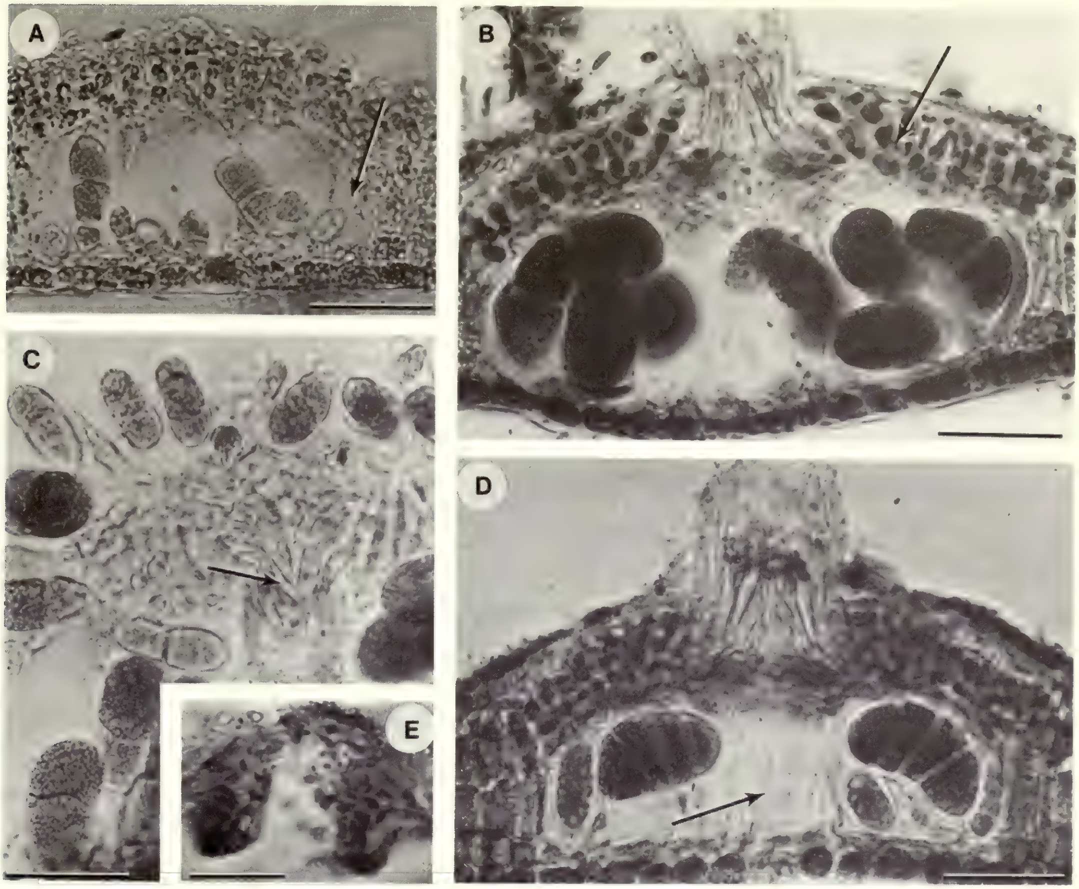

Fig. 82 Conceptacle features in decalcified crusts of *Pneophyllum zonale*. A, Vertical section of young bisporangial conceptacle grown in laboratory culture showing stretched perithallial cells (arrow). Scale = 50 μm. B, Vertical section of mature bisporangial conceptacle grown in laboratory culture; note the deep roof filaments (arrow). Scale = 50 μm. C, Surface view of ruptured bisporangial conceptacle grown in laboratory culture, showing bisporangia at various stages of maturity and ostiole filaments (arrow). Scale = 50 μm. D, Vertical section of mature tetrasporangial conceptacle from Bembridge growing on *Chondrus*; note central sterile paraphyses (arrow). Scale = 50 μm. E, Vertical section of carposporangial ostiole from slide of type material of *Fosliella tenuis* (Adey & Adey, slide no. 67-16, 50–7E). Scale = 20 μm.

lumina, the filaments terminate in domed epithallial cells. The remnants of the upper parts of perithallial cells which give off the roof filaments are shown in Figure 83, while the position which they held can be deduced in an S.E.M. preparation of the underside of the conceptacle roof (Fig. 11E), in which the rows of pit connections indicate the site at which each roof filament was given off; the elaborate nature of the pit plug can also be seen in this material (Fig. 11A). The ostiolar filaments (Figs 81B; 83) are very well developed in *P. zonale*; the downward filaments are robust and plentiful, while the upward filaments are long and characteristically wispy, appearing to taper off indefinitely at the apex as is indicated in their S.E.M. appearance previously described. In VS the ostiolar filaments appear to dip down before rising up through the ostiole, where they form a criss-cross pattern (Fig. 81B). These features are also seen in Rosenvinge's (1917) drawings and specimens (C) of *Melobesia trichostoma* and are instantly recognisable features of *Pneophyllum zonale*.

Young bisporangia (Fig. 82A, C) are more or less farctate and develop peripherally on stalk

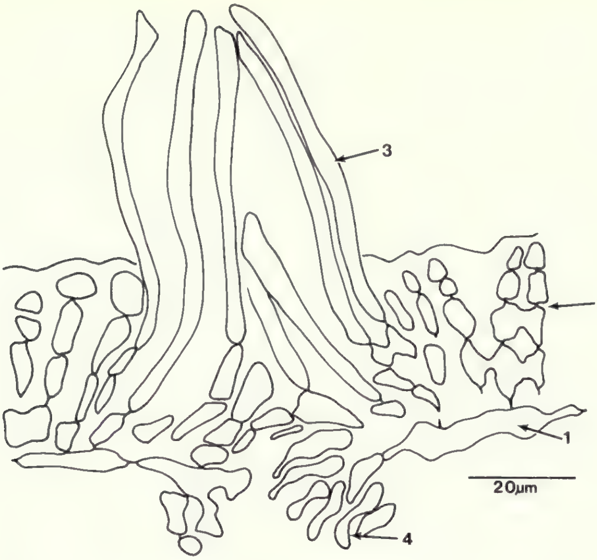

Fig. 83 Roof and ostiole structure of bisporangial conceptacle of *Pneophyllum zonale*. 1 = shrivelled remains of perithallial cell; 2 = deep roof filaments; 3 = upward ostiole filaments; 4 = downward ostiole filaments.

cells on the conceptacle floor; the central sterile filaments may be swollen in young material but collapse and become tenuous in older specimens. Mature conceptacles are crowded with up to about 60 bisporangia which, on release, are noticeably pear-shaped, which is a further characteristic of *P. zonale*.

PHENOLOGY: Little is known about the seasonal occurrence and reproduction of *P. zonale* on the shore. Specimens collected at various times of year were all bisporangial, except for the single epiphytic gametangial plant which was collected in February, and epiphytic tetrasporangial crusts collected in August and November. In laboratory culture (Chamberlain, 1982) *P. zonale* did not grow very well but a bispore which germinated in September formed a crust which took 160 days to produce mature spores over the winter months, while one which germinated in February took only 95 days. This suggests that warmer and/or longer daylength conditions stimulated growth and reproduction.

FORM RANGE: Insufficient material has been collected to permit any observations on form range on the shore, although conceptacles grown in culture tended to be larger than those collected from the shore. In culture (Chamberlain, 1982), trichocytes were produced only between May and September and were absent during the winter.

DISTRIBUTION:
British Isles: P. zonale is known only from Hampshire, Dorset, Devon and Anglesey at present, but is probably widely distributed.
World: Norway, Denmark, France, Italy, southern Australia (W. J. Woelkerling–pers. comm.).

HABITAT: *P. zonale* is predominantly an epilithic or epizoic species occurring on glass, pebbles, and mollusc shells. It occurs as an epiphyte fairly often on *Chondrus crispus* and has been recorded once on *Halopitys incurvus*. In Australia it is a sea-grass epiphyte.

LIFE HISTORY: The bisporangial plant is self-perpetuating (Chamberlain, 1982); the bispores are presumably diploid.

Table 28 Dimensions of vegetative structures (in μm unless stated).

Pneophyllum zonale	British Isles	Hamel & Lemoine (1953)	Adey & Adey (1973) (*Fosliella tenuis pro parte*)	Crouan type specimen
crust diameter	up to 10+ mm	2–10 mm		
crust depth	up to 130	up to 70		
crust cell length	(10) 14 (17)	9–14 (20)	8·5–18·5	12–18
surface width	(5) 9·5 (13·5)	7–10 (12)	8–16	3·6–10
crust cell height	*c.* 12			
epithallial cell length	(3·5) 5 (6·5)		4·5–6·5	5·5
surface view width	(4) 6·5 (9·5)		4·5–6·5	5·5
epithallial cell height	*c.* 6			
hypothallial cell width				
VS height				
perithallial width	(7) 10·5 (14·5)			10–14·5
cell height	(10) 15 (28·5)			13–19
VS number	up to 8	up to 9		
trichocyte type	branch cell and intrafilament	intercalary		branch cell and intrafilament
trichocyte length	20–30			25
surface view width	11–14			12

RIDGWAY COLOUR CODE: dry crust – rocellin purple, pl. XXXVIII

12. Pneophyllum sargassi (Foslie) Y. Chamberlain, comb. nov.

BASIONYM: *Melobesia marginata* forma *sargassi* [‘*Sargassii*’] Foslie in *K. nor. Vidensk. Selsk. Aarsberetn.* **1903**: 22 (1904).

NOMENCLATURAL SYNONYMS: *Lithophyllum* (subgenus *Carpolithon*) *sargassi* (Foslie) Foslie in *K. nor. Vidensk. Selsk. Skr.* **1906** (2); 26 (1906).

Melobesia (subgenus *Pliostroma*) *sargassi* (Foslie) Foslie in *K. nor. Vidensk. Selsk. Skr.* **1908** (11): 6 (1908).

Heteroderma (subgenus *Pliostroma*) *sargassi* (Foslie) Foslie in *K. nor. Vidensk. Selsk. Skr.* **1909** (2): 57 (1909).

REFERENCES: *Melobesia sargassi* (Foslie) Foslie; Masaki & Tokida in *Bull. Fac. Fish. Hokkaido Univ.* **14**: 4 (1963); Adey & Lebednik, *Catalog of the Foslie herbarium*: 37 (1967).

Heteroderma sargassi f. *sargassi* Masaki in *Mem. Fac. Fish. Hokkaido Univ.* **16**: 25 (1968); Adey in *K. nor. Vidensk. Selsk. Skr.* **1970** (1): 17 (1970); Park in *Bull. natn. Fish. Univ. Busan* **20**: 19 (1980).

Heteroderma sargassi f. *parvula* Masaki in *Mem. Fac. Fish. Hokkaido Univ.* **16**: 26 (1968); Park in *Bull. natn. Fish. Univ. Busan* **17** (1, 2): 61 (1977), in *Bull. natn. Fish. Univ. Busan* **20**: 20 (1980).

SPECIMENS: Although no herbarium material of *Pneophyllum sargassi* as such was available, a search through BM specimens of the principal host *Halopitys incurvus* yielded a number of records: Pulteney, Plants of Dorset; Mrs Griffiths, November 1927, Sidmouth; Schiffner, Alg. Mar. 1402, July 1928, Trieste; S. Pignatti, 13 July 1966, Trieste; and many specimens from Brittany and Normandy.

HOLOTYPE: TRH Yendo, April 1903, Misaki, Japan, on *Sargassum serratifolium* (not seen, but see remarks below on the identity of this material).

DIAGNOSIS: Epiphytic species, almost exclusively on *Halopitys*, with thallus up to 13 cells deep, zonal conceptacles and simple ostiole: differing from *P. rosanoffii* in not having free ostiolar filaments; from *P. microsporum* in having zonal conceptacles; from *Melobesia membranacea* in having a deep thallus and single-pored sporangial conceptacles; and from *Fosliella farinosa* in having a deep thallus and lacking terminal trichocytes.

Table 29 Dimensions of reproductive structures (μm unless stated).

Pneophyllum zonale	British Isles	Rosenvinge (1917) (*Melobesia trichostoma*)	Hamel & Lemoine (1953)	Adey & Adey (1973) (*Fosliella tenuis*)	Crouan type specimen
CARPOSPORANGIAL CONCEPTACLE					
external diameter			210–300		
surface diameter					
VS internal diameter	135 (1 only)	123		72–108 [130]	
VS height	73	83	100–200	53–78	
VS roof height	16				
roof type	irregular				
no. basal cell rows	2				
ostiole	long filaments	long filaments			
no. gonimoblast filaments					
diameter carpospore			30–40×20		
SPERMATANGIAL CONCEPTACLE					
VS/surface width		45		32 [50]	
VS height					
length spermatium					
width spermatium					
TETRASPORANGIAL CONCEPTACLE					
external diameter			140–250		up to 300
surface diameter					
VS internal diameter	(156) 202 (240)	154		106–135	180–200
VS height	(78) 86 (99)	131	120–150	78–96	
VS roof height	(26) 29 (34)				
roof type	irregular				
no. basal cell rows	1–2				
ostiole	long filaments	long filaments			
no. tetrasporangia					
length tetrasporangium	(49·5) 57·5 (74)	52·5	45–60		40
width tetrasporangium	(26) 32·5 (41·5)	24·6	40		23
BISPORANGIAL CONCEPTACLE					
external diameter					
surface diameter	(169) 189 (234)				
VS internal diameter	(96) 193 (260)				
VS height	(65) 92 (117)				
VS roof height	(18) 29 (39)				
roof type	irregular				
no. basal cell rows	up to 3				
ostiole	long flattened filaments				
no. bisporangia	up to 60+				
length bisporangium	(41·5) 57 (73)		85		
width bisporangium	(26) 29 (34)		30		

DESCRIPTION: Small, obscure, milky grey crusts up to 2 mm diameter, 200 μm deep, perithallium up to 12 cells deep in crust centre and usually present at periphery, *perithallial cells* (in VS) irregular, 5·5–10·5 μm wide × 7–16·5 μm high, *crust cells* in surface view oblong, 10–13·5 μm long × 3·5–7·5 μm wide, *epithallial cells* 3–5·5 μm long × 3–5·5 μm wide, *trichocytes* not seen; conceptacles somewhat raised, all except spermatangial conceptacles with simple ostiole and zonal roof, *carposporangial conceptacles* 72–130 μm internal diameter × 48–95 μm high, mature fusion cell narrow and deep, *spermatangial conceptacles* immersed (often deeply) beside carpogonial conceptacles, 28–59 μm wide × 19–44 μm deep, ostiole prolonged into a spout, *tetrasporangial conceptacles* 78–122 μm internal diameter × 66–106 μm high, tetrasporangia borne peripherally, up to *c*. 8 per conceptacle, 39–65 μm long × 26–50 μm wide, *bisporangial conceptacles* unknown.

HISTORICAL: *Pneophyllum sargassi* was described by Foslie (1904*c*, as *Melobesia marginata* f. *sargassi*) on material growing on *Sargassum serratifolium* in Japan. Masaki & Tokida (1963 as *Melobesia*) recorded it from Japan growing on *Sargassum* spp. and *Laurencia intermedia*. They noted that plants growing on *Laurencia* and the stems and leaves of *Sargassum* were 3–8 cells deep below the conceptacles, while those growing on *Sargassum* vesicles were only from one to a few cells deep. Masaki (1968 as *Heteroderma*) later described the plants growing on *Laurencia* as a distinct form (f. *parvula*) which differed from f. *sargassi* in having smaller tetrasporangial and carposporangial conceptacles. The taxon described by Masaki & Tokida (1963) is well defined, but the identity of the type specimen (TRH) is in some doubt; Adey (1970), for example, comments 'Lectotype: in the original description, only Japan is given for a locality. However, this is the only specimen in the collection', unfortunately he does not give data for the specimen. Adey & Lebednik (1967), on the other hand, catalogue only one specimen of the entity as 'Yendo, Japan, Misaki, 4. 1903'. Masaki & Tokida (1963) received material from what was believed to be the type specimen in Trondheim which proved to be *Fosliella farinosa*; they gave no collection data but it would presumably have been the Yendo specimen.

CRUST APPEARANCE: This species forms lightly calcified, deep (up to 200 μm) crusts which usually grow epiphytically on *Halopitys incurvus* (Fig. 84A) together with *P. rosanoffii* and *M. membranacea*. When fresh, the crusts are a milky grey colour which, despite their considerable depth, have an unsubstantial appearance; the conceptacles are small, rounded, and dark in the centre. In dried material the vegetative crust becomes invisible against the dark background of the host, and only dark-centred conceptacles can be seen. It is difficult to measure the crust diameter but it probably does not exceed 2 mm.

Under the S.E.M. it was not possible to find the crust edge to describe cell shape, since the whole area of the crust was occupied by conspicuous, rounded conceptacles (Figs 84A, B); in air dried material (Figs 84B, D) the roof of the conceptacle is occupied by more or less isodiametric cells with calcified rims and large, central, epithallial concavities, the cells may be partially covered with a smooth coating and the ostiole is small and simple. In critical point dried material (Figs 84A, C), the central area of the roof with the isodiametric cells has a thick covering, while the original crust cells form a distinctive ring at the conceptacle base; the ostiole is closed by a thick, mucilage plug. The spermatangial conceptacle (Fig. 84A) is situated in the side of the carposporangial conceptacle.

Material from Japan kindly sent by Dr Masaki has much larger crusts (up to 30 mm diameter), and under the S.E.M. the air dried conceptacles have more conspicuous central cells, although the roof appears to be zonal as in British material.

VEGETATIVE ANATOMY: *P. sargassi* has a deep thallus which rarely has a thin border so that it is difficult to see crust cells in surface view, but when they are visible they are elongated and have rounded epithallial cells. The perithallium usually develops immediately behind the first meristem (Fig. 88A). It is composed of cells which vary from isodiametric to vertically elongated which tend, at least in the deeper crust, to be irregularly arranged rather than appearing to fall in horizontal rows. The perithallial filaments may be up to 12 cells deep; the uppermost (second

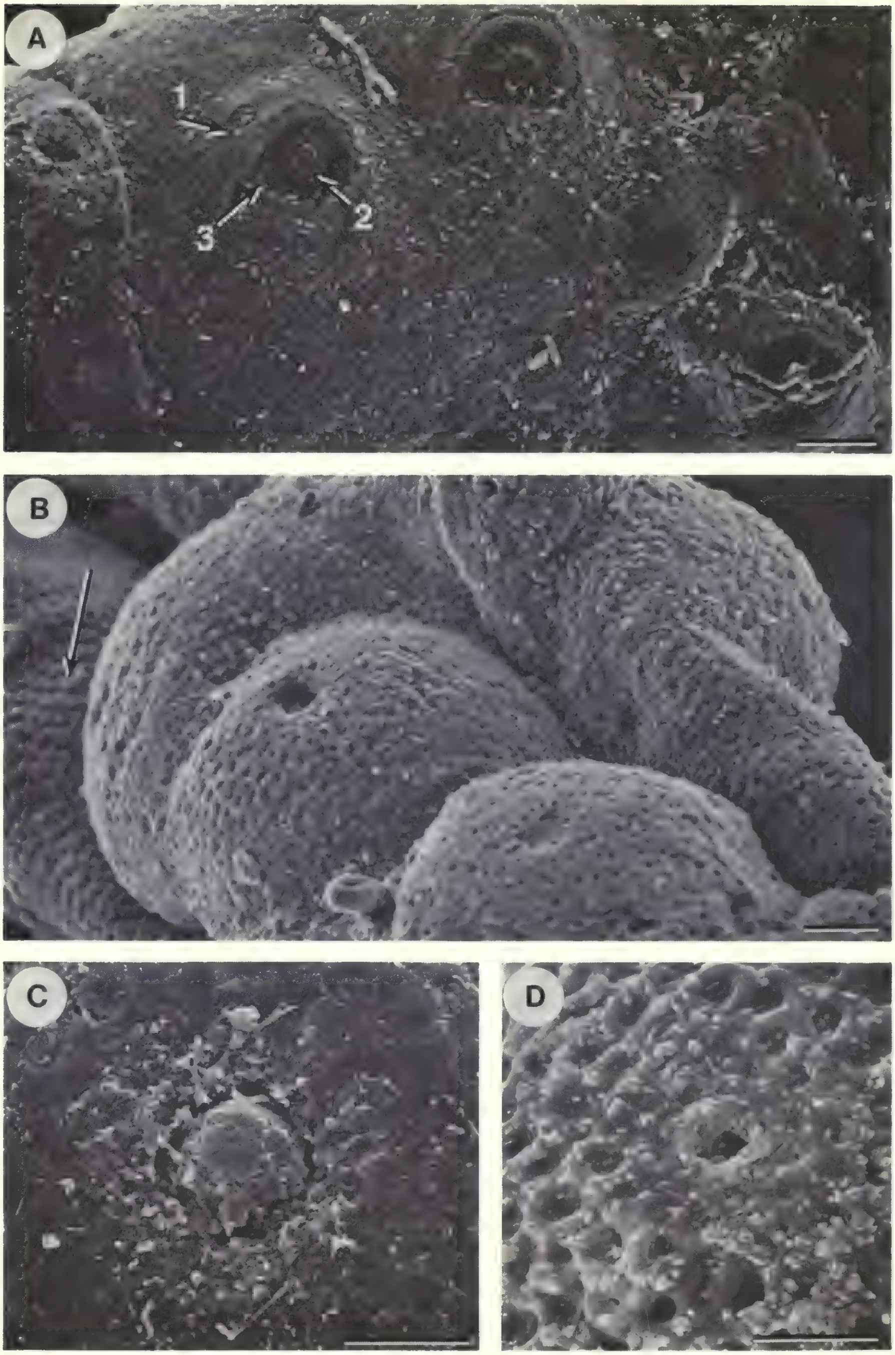

Fig. 84 Scanning electron micrographs of *Pneophyllum sargassi.* A, Gametangial crust critical point dried showing spermatangial (1) and carposporangial (2) conceptacles and rim of original thallus surface round conceptacle base (3). Scale = 100 μm. B, Air-dried crust growing adjacent to *Melobesia membranacea* (arrow). Scale = 50 μm. C, Conceptacle roof from A with mucilage plug in ostiole. Scale = 25 μm. D, Conceptacle roof from B showing isodiametric shape of roof cells. Scale = 25 μm.

meristem) cell may be squat or tall and tapering depending upon how recently it has divided. The epithallial cell is flattened or triangular in vertical section and occasionally two to three-celled epithallial filaments develop – the only British species of *Pneophyllum* in which this occurs. Trichocytes have not been found in British material of *P. sargassi*, and Masaki (1968) did not find any in Japanese material. The cell dimensions and general shape and arrangement agree well with Masaki's (1968) description.

GAMETANGIAL PLANTS: English plants are monoecious. Spermatangial conceptacles (Figs 84A; 85A, F; 86C; 87) are immersed in the thallus beside the carpogonial conceptacles, the ostiole is prolonged into a spout, and often the conceptacles are so deeply buried within the perithallium that the spout traverses a considerable depth of crust before emerging on the surface. The spermatangial initials cut off elongate spermatangia (Fig. 87), which become more or less oval when released and are relatively large, measuring up to 6·5 μm long. The material described by Masaki & Tokida (1963) appears from their illustrations to be dioecious, as were the crusts on the slide loaned by Dr Masaki. The Japanese conceptacles are larger and relatively wider than the English ones taking into account the inclusion of the spout in the dimension given by Masaki & Tokida (1963) for conceptacle height.

Stages in carpogonial conceptacle development observed in English material correspond closely with those described and illustrated by Masaki & Tokida (1963). When a conceptacle is initiated (Fig. 86A), the perithallial cells beside the fertile disc swell and elongate, while those above the disc disintegrate. The procarps (Figs 85B; 86B, C) are borne on a conceptacle base up to four cells deep; Figures 86E–H show three sections through the parts of the fertile disc as shown, which indicate that the central procarps (Fig. 86H) bear single carpogonia, while the peripheral structures (Figs 86F, G) are simpler and may lack fertile cells. Masaki & Tokida (1963) recorded one or two carpogonia per procarp, but their illustrations show only single ones. As the conceptacle develops, very pronounced growth occurs round the ostiole (Figs 85B; 86B), which becomes deeply invaginated, while the old thallus surface is pushed back from the conceptacle centre allowing the new roof structure to emerge.

CARPOSPORANGIAL CONCEPTACLES: The carposporangial conceptacles (Figs 85E; 86D) are rounded and somewhat prominent. The centre of the roof emerges entirely through the thallus surface, the remains of which form a ring round the conceptacle base (Fig. 84A). The ostiolar area, which appeared very invaginated in the carpogonial conceptacle, finally rises to the surface, so that the mature ostiole is simple and often conspicuously plugged with mucilage (Figs 84C; 86D). The conceptacle roof in VS is composed of three rather regular cell layers (Fig. 86D):– the epithallium, a layer of tall cells, and an internal layer of flattened cells. The fusion cell is rather narrow and deep (Figs 85D; 86D), and often appears to be in open contact with the subtending cells (Fig. 85C); the carposporangial filaments are developed peripherally. In mature conceptacles (Fig. 85E) the fat fusion cell is often situated high in the conceptacle chamber.

TETRASPORANGIAL PLANTS: Mature tetrasporangial conceptacles (Figs 88B; 89B) are similar to carposporangial conceptacles in appearance, but seem to develop much more simply without the deeply invaginate stages seen in carpogonial conceptacles. The tetrasporangia are borne peripherally on stalk cells; the young ones are deeply invaginate (Figs 88A; 89A) with the four nuclei often being clearly visible, and the tetrasporangium apparently goes through an unstructured later phase (Masaki & Tokida, 1963, Pl. IX, Fig. 6) before finally maturing and becoming farctate. The ostiole (Fig. 89A) is simple.

BISPORANGIAL PLANTS: Unknown.

PHENOLOGY: Crusts are found throughout the year growing on intertidal plants of *Halopitys incurvus*, but *P. sargassi* is most abundant and in best condition between about September and December; at this time the crusts are thinner because they are growing more rapidly and the sporangia are clear and healthy looking. In very cold periods and in summer the crusts are

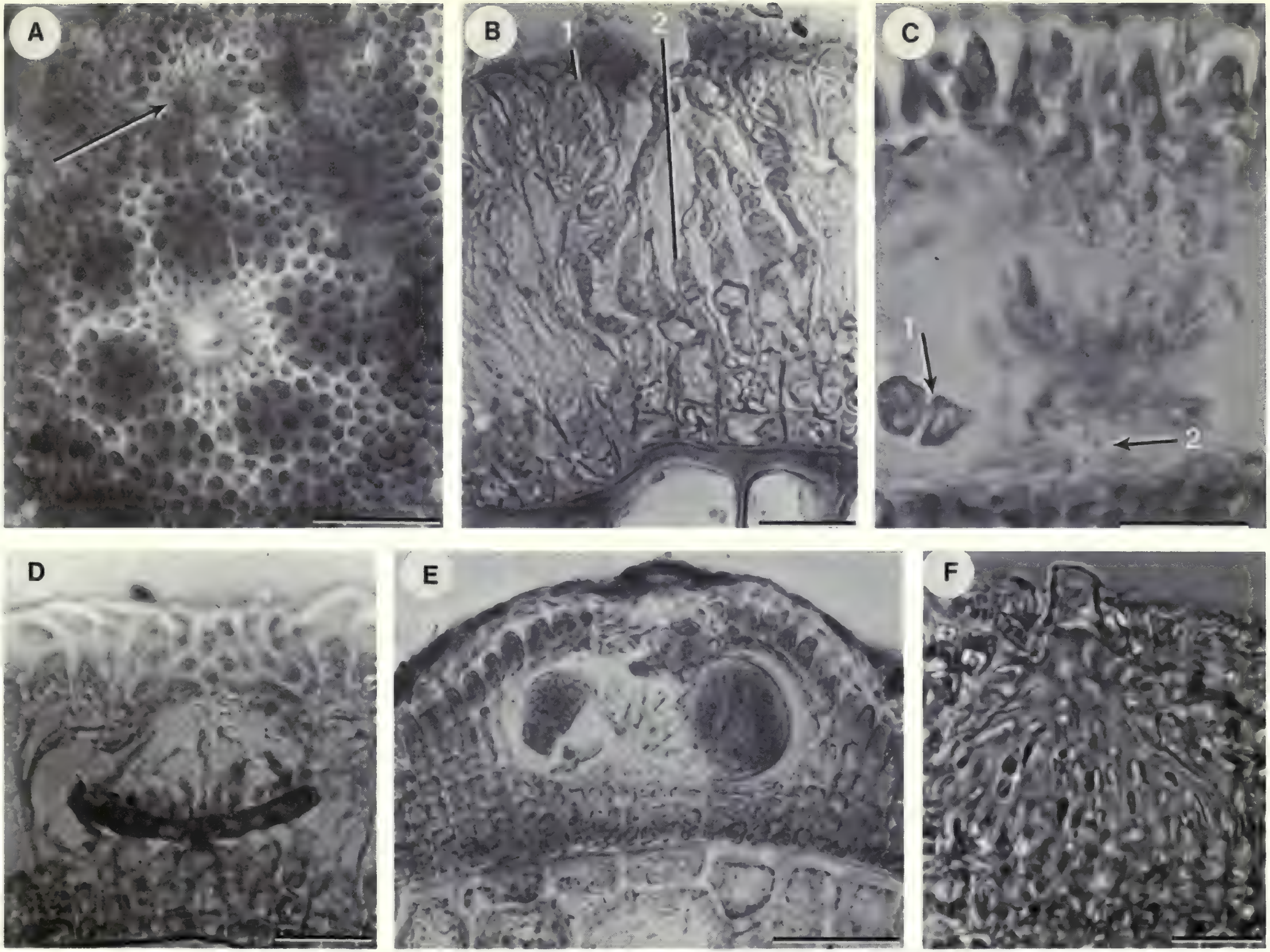

Fig. 85 Gametangial and carposporangial conceptacles in decalcified material of *Pneophyllum sargassi*. A, Surface view of carposporangial and spermatangial (arrow) conceptacles showing the isodiametric conceptacle roof cells. Scale = 50 μm. B, Vertical section of carpogonial conceptacle showing developing roof filaments (1) and procarps (2). Scale = 20 μm. C, Vertical section of developing carposporangial conceptacle to show young gonimoblast filament (1) and connection between fusion cell and subtending cell (2). Scale = 20 μm. D, Vertical section of early carposporangial conceptacle to show fusion cell. Scale = 20 μm. E, Vertical section of carposporangial conceptacle to show fusion cell high in conceptacle chamber. Scale = 25 μm. F, Vertical section of spermatangial conceptacle. Scale = 20 μm.

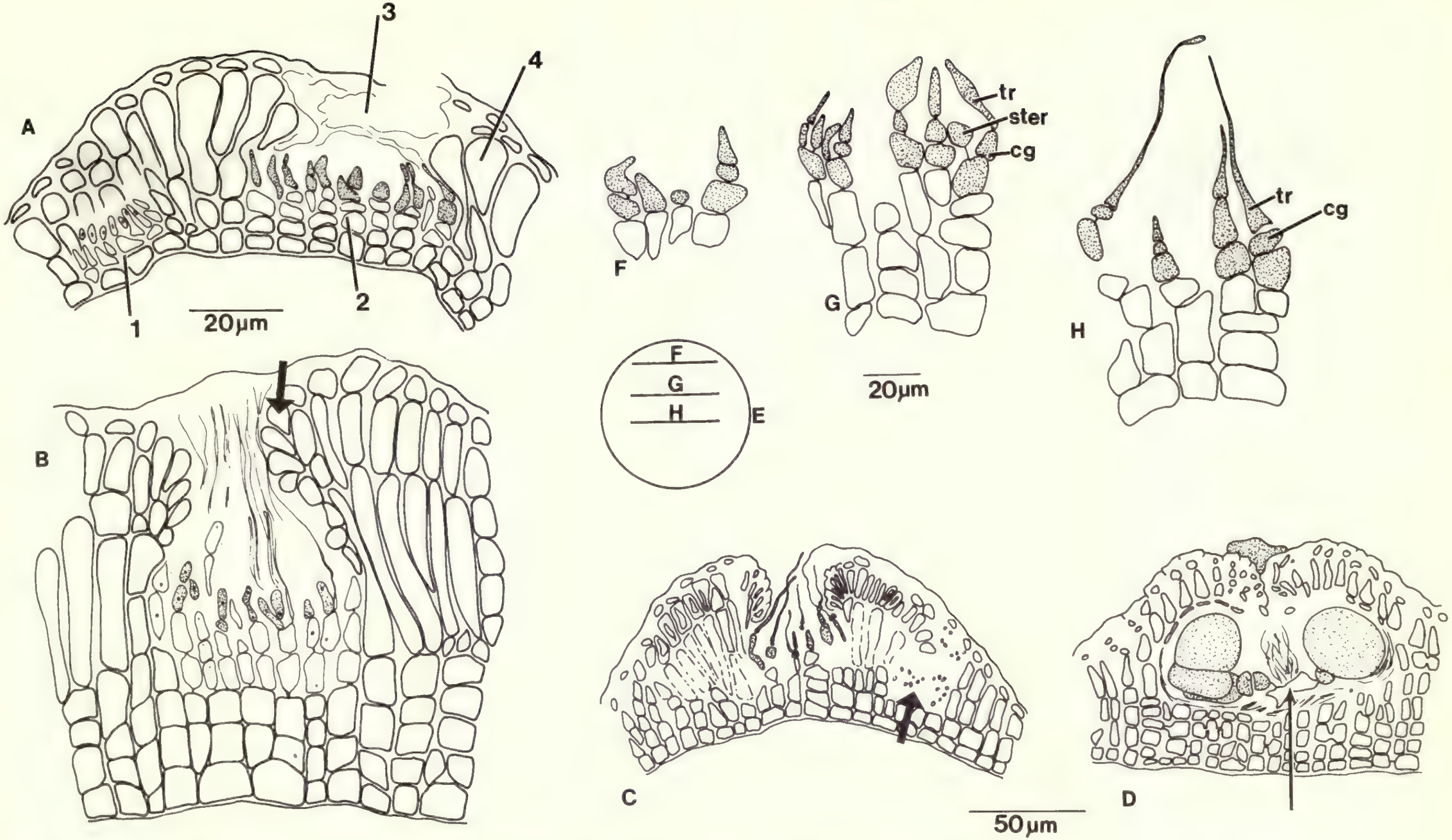

Fig. 86 Vertical sections of carpogonial and carposporangial conceptacles of *Pneophyllum sargassi.* A, Young spermatangial conceptacle (1) and young carpogonial conceptacle (2) showing the disintegration of the thallus surface (3) and the swollen perithallial cells (4). B, Mature carpogonial conceptacle with developing roof cells (arrow). C, Carpogonial and spermatangial (arrow) conceptacles with deeply invaginated ostiole. D, Mature carposporangial conceptacle showing the deep fusion cell (arrow) lying high in the conceptacle. E, Diagram of fusion cell indicating position from which the procarps F, G, and H were sectioned. F, Reduced peripheral procarps. G, Procarps with carpogonia, reduced trichogynes, and sterile cells. H, Procarps with single carpogonia and trichogynes.

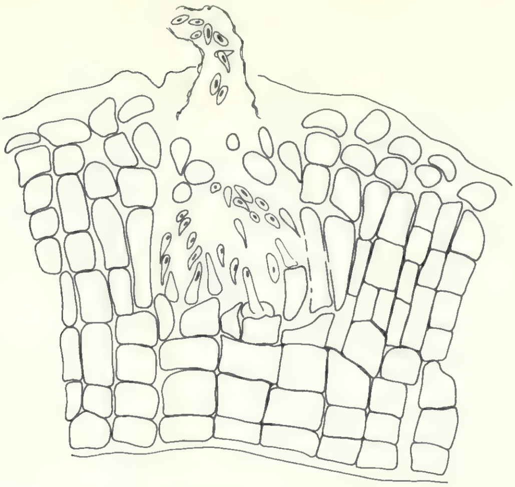

Fig. 87 Vertical section of spermatangial conceptacle of *Pneophyllum sargassi*.

thicker, more heavily calcified, and the spores are often degenerate or absent. Differences are also noted from year to year and *P. sargassi* was, for example, more abundant in 1978 than in 1979.

FORM RANGE: The British Isles material compares well with Japanese material as described by Masaki & Tokida (1963) and material kindly sent by Dr Masaki; of the two forms described by Masaki (1968) the conceptacle dimensions agree most closely with f. *parvula* (Tab. 31); however, until further European material is available for comparison it seems preferable not to distinguish forms in the present sample.

DISTRIBUTION:
British Isles: Hampshire, Dorset, Devon.
World: France, Italy, Japan.

It seems probable that *P. sargassi* is more widely distributed than is indicated above, but it is not an easy species to find and may have been missed elsewhere. The records from France and Italy were acquired by examining specimens of *Halopitys incurvus* in the British Museum; it was found on many plants from Normandy and Brittany, one plant from Biarritz, and two plants from Trieste.

HABITAT: In England, *P. sargassi* is almost entirely restricted to the host *Halopitys incurvus*. On only one occasion it was found on *Palmaria palmata*, at a time (October 1978) when it was generally much more abundant than usual. When growing on *Halopitys, Pneophyllum sargassi* is always accompanied by *Melobesia membranacea*, which it frequently overgrows (Fig. 84B). *Pneophyllum rosanoffii* also commonly occurs on *Halopitys* together with the other two species.

In Japan *P. sargassi* grows mainly on species of *Sargassum* and *Laurencia*. Although *Sargassum muticum* has become extremely abundant at Bembridge in recent years, *Pneophyllum sargassi* has never been found on this plant.

TAXONOMIC NOTE: The taxon is here classified as a *Pneophyllum* with some doubt since it shows some features not entirely typical of that genus but which seem to bear some relationship to *Fosliella*. At present, almost all known *Fosliella* species lack a vegetative perithallium and bear terminal hypothallial trichocytes, while no trichocytes have been observed in *Pneophyllum sargassi* and a deep perithallium is present. However, the single recorded exception in the genus *Fosliella* is a drawing of Japanese material of *F. farinosa* by Masaki & Tokida (1960, Pl. VI, Fig.

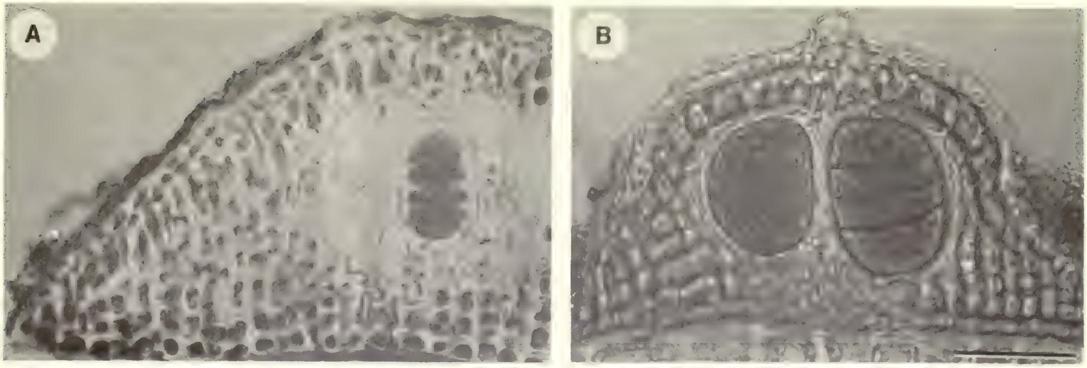

Fig. 88 Vertical sections of tetrasporangial conceptacles of *Pneophyllum sargassi*. A, Young conceptacle showing deeply invaginated tetrasporangium and deep crust periphery. B, Vertical section of mature tetrasporangial conceptacle. Scale = 50 μm.

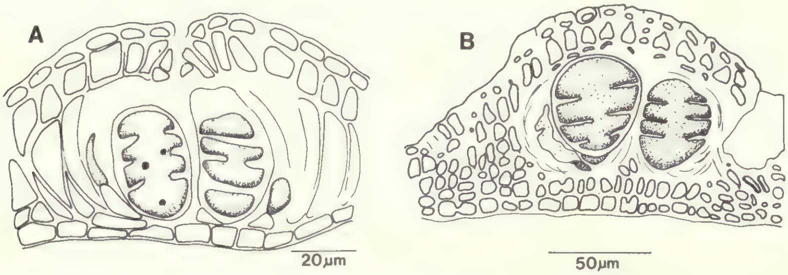

Fig. 89 Vertical sections of tetrasporangial conceptacles of *Pneophyllum sargassi*. A, Immature tetrasporangia. B, Mature tetrasporangia.

7, as *Melobesia*) which shows a tetrasporangial conceptacle which strongly resembles those of *Pneophyllum sargassi* and which was probably also growing on *Sargassum*. In addition, the elongated crust cells and rounded epithallial cells seen in present and Japanese material (Masaki

Table 30 Dimensions of vegetative structures (μm).

Pneophyllum sargassi	British Isles	Masaki (1968) (as *Heteroderma*)
crust diameter	up to *c.* 2 mm	5–10 (30)
crust depth	up to 200	97–126
crust cell length	(10) 11·5 (13·5)	12–20
surface width	(3·5) 6 (7·5)	5–8
crust cell height	6–7	5–7
epithallial cell length	(3) 4 (5·5)	12–20 (?)
surface view width	(3) 4·5 (5·5)	5–8
epithallial cell height	2–4	5–7
hypothallial cell width		5–7 (10)
VS height		9–12 (17)
perithallial width	(5·5) 8 (10·5)	7–11
cell height	(7) 11 (16·5)	9–21
VS number	up to 12	up to 12
trichocyte type		
trichocyte length		
surface view width		

Table 31 Dimensions of reproductive structures (μm).

Pneophyllum sargassi	British Isles	Masaki (1968) f. *sargassi*	Masaki (1968) f. *parvula*
CARPOSPORANGIAL CONCEPTACLE			
external diameter		(42) 84–134 (172)	75–100
surface diameter	(83) 101 (130)		
VS internal diameter	(72) 98 (130)		
VS height	(48) 72 (95)	50–80	50–75
VS roof height	(15) 23 (33)	12–21	
roof type	zonal	zonal	zonal
no. basal cell rows	1–4		
ostiole	simple	simple	simple
no. gonimoblast filaments	*c.* 8		
diameter carpospore			
SPERMATANGIAL CONCEPTACLE			
VS/surface width	(28) 43 (59)	60–92	
VS height	(19) 32 (44)	25–84	
length spermatium	(3·5) 4·5 (6·5)	4	
width spermatium	(1·5) 2 (2·5)	1·7	
TETRASPORANGIAL CONCEPTACLE			
external diameter		140–210	75–100
surface diameter	(110) 132 (160)		
VS internal diameter	(78) 100 (122)		
VS height	(66) 82 (106)	50–105	65–85
VS roof height	(14) 21 (26)		
roof type	zonal	zonal	zonal
no. basal cell rows	1–4		
ostiole	simple	simple	simple
no. tetrasporangia	up to *c.* 8		
length tetrasporangium	(39) 54 (65)	46–63	40–50
width tetrasporangium	(26) 39 (50)	30–42	20–30

& Tokida, 1963, Pl. IX, Fig. 4) of *P. sargassi* are similar to those seen in *Fosliella*; furthermore, judging by the fact that material from Trondheim purporting to be *Pneophyllum sargassi* proved to be *Fosliella* (*fide* Masaki & Tokida, 1963), it would seem that the taxa are easy to confuse.

A further character which suggests a relationship to *Fosliella* is the apparent absence of procarps bearing two carpogonia in English material of *Pneophyllum sargassi*. Most records of *Fosliella* indicate that this genus always has single carpogonia, while some bicarpogonial procarps are present in all *Pneophyllum* spp. Masaki & Tokida (1963) report bicarpogonial procarps in *P. sargassi*, but their drawing shows only single carpogonia; on the other hand, their illustrations of *Fosliella farinosa* (Masaki & Tokida, 1960) show bicarpogonial procarps. In addition present material of *Pneophyllum sargassi* may show connections between the fusion cell and subtending cells (Fig. 85C). These features need further investigation.

The final character of interest in the present context is the spore segmentation pattern. *Fosliella* is distinguished from *Pneophyllum* in the present study by having a four-celled central element to the germination disc, as opposed to an eight-celled one. My own attempts to germinate spores from *P. sargassi* were unsuccessful but Chihara (1974*a*) and Notoya (1976*a*) have both germinated spores and found a *Corallina*-type germination pattern which is different from both the *Fosliella* and *Pneophyllum* types. Notoya (1976*a*) found a similar pattern in species of *Neogoniolithon* and *Pseudolithophyllum* sensu Adey, which are both mastophoroid algae, and also in *Lithothamnion* which is in a different subfamily. This, therefore, seems to supply added negative evidence that *P. sargassi* may not belong to the genus *Pneophyllum*. However, it seems best to refer it to *Pneophyllum* for the present until detailed information is available to indicate its true affinities.

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